evolution

A Centre of Excellence for Civil Service Examination Guidance

B 11, Second Floor, Commercial Complex, Batra Cinema Road
Next to ICICI A.T.M., Dr. Mukherjee Nagar, DELHI - 110 009
Phone: 011 - 32974645, 32974651, 47092329

2017

BOTANY - I: GYMNOSPERMS

GYMNOPSERMS: TABLE OF CONTENTS

INTRODUCTION TO GYMNOSPERMS

An introduction to Gymnosperms

The term gymnosperm *(gymnos* = naked, *sperma* = seed) was coined by Theophrastus (372-286B.C.), for the **plants which produce seeds without fruits**.

Gymnosperm *(Gymnospermae) are a group of spermatophyte seed-bearing plants with ovules on an open sporophyll, which are not modified into flower like structure. Hence, gymnosperms are non flowering plants.*

The gymnosperms comprise of 65 genera and 1091 species (*Tree of Life Project*, 2008).

They are divided into four extant divisions:

1. Coniferophyta (the conifers),
2. Cycadophyta (the cycads),
3. Ginkgophyta (the ginkgoes), and
4. Gnetophyta (the gnetophytes).

Salient features

The major features of the gymnosperms include the following.

1. Sporophytic Plants are woody and evergreen, trees, shrubs or lianas without having any herbaceous member. The gymnosperms include the oldest and largest trees known. The Bristle Cone Pines such as *Pinus aristata* and *Pinus longaeva* (about 5000 years old) are the oldest living plants. The Giant Redwoods (*Sequoiadendron giganteum*) are more than 100 m tall - the tallest plants known. Both are native to California, the USA.
2. Plants have a tap root system, which generally persists for a long time.
3. Xylem is made up of tracheids, parenchyma and rays. Vessels are only present in some members of Gnetales.
4. Phloem consists of sieve cells only where sieve areas commonly occur on the radial wall. The companion cells are absent.
5. In many members, the albuminous cells are present in place of the companion cells in phloem tissue, but the albuminous cells are not sister cells to the sieve cells.
6. Secondary growth is present in all members, where mature metaxylem shows bordered pits.
7. All members are heterosporous, producing *microspores* which develop into pollen grains and *megaspores* which are retained in an ovule.

8. The gametophytic stage is very reduced. It is represented by a multicellular female gametophyte that develops inside the ovule and a pollen tube formed by the pollen grain. Prothallial cell is present in male gametophyte.
9. The female sex organ is archegonium. Hence, the gymnosperms are archegoniate plants.
10. The pollen grains are anemophilous that is wind despersible.
11. The development of female gametophyte shows a prolonged free nuclear phase.
12. There is a long interval between pollination and fertilization.
13. Reproduction in gymnosperms varies greatly. Cycads and *Ginkgo* have motile sperm, while conifers and Gnetophytes have sperm with no flagella. However, in all cases the sperms are conveyed to the egg along a pollen tube, which grows through ovule tissue.
14. After fertilization, the ovule develops into a seed. Ovule develops without being enclosed by ovary of a flower. Hence, after fertilization, when the ovule becomes the seed, the latter is not enclosed by a fruit. This explains the name, Gymnosperms (literally meaning, *the naked seeded plants*).
15. The seed consists of a single integument (unitegmic).
16. Endosperm is haploid (n) and produced before fertilization.
17. All the gymnosperms follow a common life cycle plan, with minor group specific variations. The generalized life-cycle plan is shown in Fig. 1.

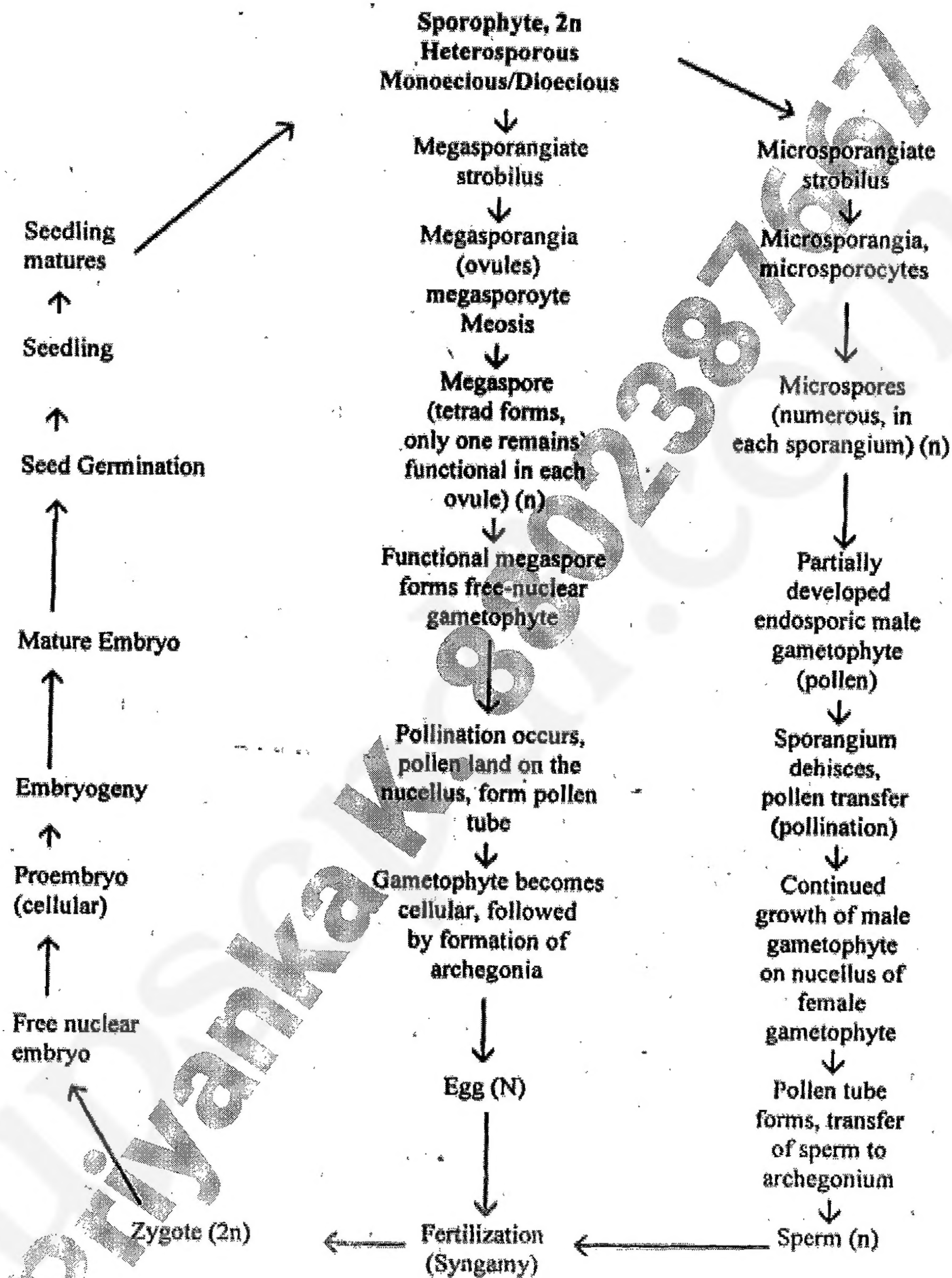

Figure 1: The life cycle of Gymnosperms

The comparison between the Gymnosperms & the Pteridophytes

Similarities:

1. The general life history of both is identical with structural differences. Both groups show a regular alternation of generations, with gradual reduction and loss of independence of the gametophyte from the higher pteridophytes to the gymnosperms, and a gradual increase in the complexity of the sporophyte.
2. The plant body is clearly differentiated into root, stem and leaves.
3. The leaves are of a compound nature and have circinate vernation, as in the cycads.
4. The xylem of the vascular bundle has only tracheids (and no vessels, except in Gnetales) and phloem without companion cells.
5. There occurs a gradual differentiation of the sporophylls (micro and mega) and of the spores-microspore and megaspore (heterosporous condition) in the higher pteridophytes, leading to complete differentiation in the gymonosperms. The segregation of the sporophylls from the vegetative region and their arrangement in the form of cones (strobili) is another development.
6. The gametophyte develop within the spore-coat as a dependent body (partially endosporous in *Selaginella* but completely endosporous in gymnosperms) for food supply and adequate protection by the sporophyte.
7. Ciliate spermatozoids develop in the lower gymnosperms (cycads), as in pteridophytes.
8. The megaspore is retained within the megasporangium (permanently in gymnosperms but only for a short period in *Selaginella*) the archegonia develop in the female gametophyte.
9. Formation of the suspensor in the gymnosperms during the stages of embryo development, as in *Selaginella*, is another similarity.

Differences:

1. Development of the ovule (and later the seed) in gymnosperms is a fundamental difference. The ovule and the seed are characteristic of all gymnosperms, while they are altogether absent in pteridophytes.
2. Formation of the pollen tube in gymnosperms is another special feature which is absent in pteridophytes. The pollen tube carries the non-motile male gametes to· the archegonium in most gymnosperms, while in all pteridophytes, the motile spermatozoids swim by themselves to the archegonium in a drop of water.
3. The megasporangium of the gymnosperm does not shed before fertilization and maturity; further, it is provided with a new structure in the form of a coat-the integument. The megasporangium covered by the integument is the ovule. The ovule is altogether absent in pteridophytes.
4. The megaspore of the gymnosperm remains permanently enclosed within the megasporangium. The female gametophyte is also completely endosporous (partially endosporous in

Selaginella) and is consequently dependent on the mother sporophyte for nourishment. The embryo also remains enclosed within the megasporangium and is nourished by it.

5. The gametophytes of gymnosperms are not green since they remain enclosed.
6. The construction of the archegonia is much simpler in gymnosperms (shorter neck and no neck canal cells) unlike in pteridophytes. Final reduction of the archegonia takes place in the higher gymnosperms, as in *Gnetum* – a feature closer to angiosperms.
7. The presence of cambium leads to secondary growth in thickness in the gymnosperms, while its absence denies secondary growth to most of the pteridophytes.

Table 1. **Distinction between Gymnosperms & Pteridophytes**

Pteridophytes	Gymnosperms
1. Main plant body is sporophyte, gametophyte is independent of sporophyte.	1. Main plant body is sporophyte. There is a reduction in the gametophytic generation which is completely dependent upon the sporophyte.
2. In sporophyte, tap root system gets lost and roots are always adventitious.	2. Sporophyte bears well-developed tap root system.
3. Both homosporous and heterosporous members are present.	3. All the members are heterosporous.
4. Secondary growth is noted in some of the members, cambium is unifacial (only produces secondary xylem inwardly).	4. Secondary growth is present in all the members, cambium is bifacial and produces both secondary xylem and secondary phloem.
5. Male gametophytes develop through endosporic proximal germination of spores.	5. Male gametophytes develop through endosporic distal germination of pollen.
6. Male gametes are motile, bi- or multiflagellated.	6. Male gametes are generally non-motile (multiflagellated, motile sperms are present only in cycads and ginkgos)
7. There is direct access of male gametes to female gametes during fertilisation.	7. During fertilisation, male gametes have to come through pollen tube, hence there is no direct access of male gametes to female gametes.
8. Megasporangium wall is dehiscent in nature, hence pteridophytes are free-sporing.	8. Megasporangium wall is indehiscent in nature, megaspore is retained within megasporangium.
9. Archegonia are comprised of neck canal cells and ventral canal cell.	9. Archegonia lack neck canal cells, and ventral canal cell is frequently eliminated.
10. Absence of seeds.	10. Presence of seeds.

The comparison between the Gymnosperms & the Angiosperms

Resemblances:

1. The plant body is differentiated into a distinct root and shoot, the latter with many branches and leaves, however small they may be. In habit, the plants of both groups may be shrubs and trees. There are more herbs among angiosperms.
2. The vascular system is well developed in both, with xylem and phloem.
3. Both develop seeds for the purpose of reproduction.

4. The microspore or pollen grain grows into a pollen tube, which carries the male gametes to a position close to the egg cell or ovum for the purpose of fertilization.
5. The megaspore remains permanently enclosed in the megasporangium (nucellus of the ovule) and germinates into the female gametophyte within the megasporangium.
6. The megasporangium remains enclosed by the integument (1 in gymnosperms and usually 2 in angiosperms), giving rise to a more complicated structure-the ovule (and later the seed) for better protection of the embryo.
7. The young sporophyte (embryo) develops at the expense of the food stored up in the parent sporophyte.

Differences:

1. In angiosperms, the xylem is composed mainly of vessels, and the phloem contains companion cells, while in gymnosperms, the xylem is made exclusively of tracheids, and phloem contains no companion cells. In higher gymnosperms, however, as in *Gnetum*, there is a combination of gymnospermic tracheids and angiospermic vessels.
2. The sporophylls are borne in strobili or cones (except the megasporophylls of cycads), whereas in angiospenns they are borne in flowers.
3. The cones of gymnosperms are much simpler than flowers in angiosperms. The cones have no calyx or corolla and they are always unisexual, consisting of either microsporophylls (stamens) or megasporophylls (carpels) only. The plants may be either monoecious or dioecious. The stamens and carpels are much simpler than in angiosperms.
4. The only agency of pollination in gymnosperms is air current, while there are many pollinating agents in the case of angiosperms.
5. In gymnosperms, the ovules are borne freely exposed on the megasporophyll (carpel), while in angiosperms, the ovules remain enclosed in the ovary, the carpel itself being differentiated into ovary, style and stigma.
6. For pollination in gymnosperms, pollen grains enter the micropyle and are deposited on the nucellus; whereas in angiosperms they are deposited on the stigma.
7. In angiosperms and higher gymnosperms, the male gametes contained in the pollen tube are two passive units, but in lower gymnosperms (*Cycas, Zamia* and *Ginkgo*), the male gametes are in the nature of ciliate spermatozoids.
8. In gymnosperms, the male gametophyte is represented by a few cells (usually 2 or 3)-a vestigial prothallus. In angiosperms, it is reduced to two nuclei-the tube nucleus and the generative nucleus. In fact, there is no evidence of a male prothallus in angiosperms.
9. The female gametophyte in gymnosperms is a relatively large structure with distinct archegonia embedded in it, each with an ovum. In angiospenns, however, the female gametophyte is represented by an 8-nucleate embryo-sac, and the ovum or egg-cell is free in it without any archegonium.

10. The endosperm, when present in the angiospenn, is fonned from the definitive nucleus only after fertilization and is mostly triploid in nature. In gymnosperms, the endosperm is formed from the vegetative tissue of the female prothallus before fertilization and is haploid in nature.
11. The seeds in all gymnosperms are endospermic, while in the members of angiopsermic families Orchidaceae, Podostemonaceae and Trapaceae, non-endospermous seeds are formed.
12. There are 2 to 15 cotyledons in gymnosperms, and 1 or 2 angiosperms.

PROGYMNOSPERMS

Introduction

The Progymnosperms constitute a group of extinct plants, mostly of Middle and Upper Devonian age, with certain anatomical characters normally associated with Gymnosperms, but without seeds.

Due to their reproduction based on spores (and not on seeds), the Progymnosperms have been considered as a group of pteridophytes. At the same time, the presence of anatomical features of the Gymnosperms makes this group unique. Many botanists conclude that the Progymnosperms are the ancestral group to the Gymnosperms.

Discovery

This group was first proposed by Charles B. Beck (1960) to describe the fossil plants with anatomical features of Gymnosperms and reproduction of pteridophytes. Charles B. Beck discovered the group in 1960 when he observed an organic connection between two Devonian fossils, namely *Archaeopteris* (a large leaf fossil with fern like characters) and *Callixylon* (a trunk fossil with Gymnospermous wood) from a museum specimen. Beck demonstrated that *Callixylon* and the leaves known as *Archaeopteris* were actually part of the same plant.

Origin of Progymnosperms

It is believed that the **Trimerophytes** were the stock ancestors to the Progymnosperms.

Trimerophytes are superficially similar to the Rhyniophytes but show some unique features not found in the Rhyniophytes.

Like the rhyniophytes,

- trimerophytes lacked leaves and roots;
- most of their plant body consisted of branching photosynthetic stems
- they had vascular tissue forming a protostele.

However,

- Trimerophytes branched pseudomonopodially, while Rhyniophytes branched dichotomously
- Some trimerophytes also bore enations - small flaps of tissue lacking vascularization, and therefore not true leaves -- on the main stems, giving them a superficially "thorny" appearance.

Salient features of the Progymnosperms

1. Progymnosperms were important components of the vegetation from the Middle Devonian through the Lower Mississipian.

2. Like the true Gymnosperms, Progymnosperms commonly had secondary growth of their vascular tissues (i.e. they produced wood), and some grew to be tall trees. Unlike the Gymnosperms however, they did not produce seeds, but rather released their spores like ferns.
3. Many of the Progymnosperms were shrubs. Yet, some Progymnosperms are known to have been tall trees with stout trunks made up of dense secondary wood, showing *pycnoxylic condition.*
4. Many of the Progymnosperms had secondary phloem while cambial activity in woody ferns, lycopods and calamites never produced any secondary phloem.
5. Ultimate branch systems were either naked or bearing small lateral appendages showing varying degrees of flattening.
6. Many of the Progymnosperms were originally thought to have had large fern-like fronds, and were indeed given generic names that were intended to suggest affinities with the ferns, e.g. *Protopteridium* and *Archaeopteris*. Subsequently, however, it has been shown that the 'fronds' were merely branch systems which were arranged in one plane like those of many modern conifers, or else became flattened during fossilization.
7. Spore production was homosporous or heterosporous, depending on the group. The heterosporous group are thought to be ancestors, or at least close relatives, of the seed plants.

Diversity of the Progymnosperms

The Class Progymnospermopsida consists of three orders, viz.

1. Aneurophytales – including genera like *Aneurophyton*, *Eospermatopteris*, *Rellimia*, *Protopteridium*, *Tetraxylopteris*, *Sphenoxylon*, *Triloboxylon*, *Proteokalon*
2. Archaeopteridales – including genera like *Archaeopteris, Pitys, Archaeopitys, Actinoxylon*, *Actinopodium*, *Svalbardia, Eddya*, and *Siderella.*
3. Protopityales – including a single genus *Protopitys*

1. **Aneurophytales** (Middle to Upper Devonian) are commonly considered the most primitive of the Progymnosperms and form an evolutionary intermediate between the trimerophyte plants the heterosporous Progymnosperms like *Archaeopteris*. The most common member of the Aneurophytales is *Aneurophyton*. It is found in rocks of Middle and Upper Devonian age. This plant resembles some trimerophytes.
2. **Archaeopteridales** lived during the Late Devonian through Early Mississippian. The order includes the genera *Archaeopteris* which has been extensively investigated, *Actinoxylon*, *Actinopodium*, *Svalbardia, Eddya*, and *Siderella.*
3. **Protopityales** were erect shrubs/trees with stems greater than 0.45 m in diameter, known from the Early Carboniferous. The stem displays endarch maturation, and the wood is composed of tracheids with circular bordered pits [a feature of Cycads]. Reproduction was fern-like with the development of spores. Most specimens are homosporous, although two size classes of spores have been identified and heterospory cannot be ruled out.

Description of *Archapeopteris*

The features the well studied specimen *Archaeopteris* (Figure 1) are listed below.

a. *Archaeopteris* at maturity was a tree, 18 m high, with a crown of spirally arranged bipinnate fronds.

b. *Archaeopteris* showed perennial growth.

c. Leaves were like a fern having large fronds where fertile and sterile pinnae were borne on the same rachis. These pinnae, in turn, bore pinnules.

d. Two rows of adaxial fusiform sporangia were present on fertile pinnules.

e. There were two types of leaves: webbed and planar leaves.

f. *Archaeopteris* also shed the leaves during the dry season. Thus, it was a deciduous tree. Because *Archaeopteris* had perennial growth buds, it tended to shed its leaves and then regrow them at a later time.

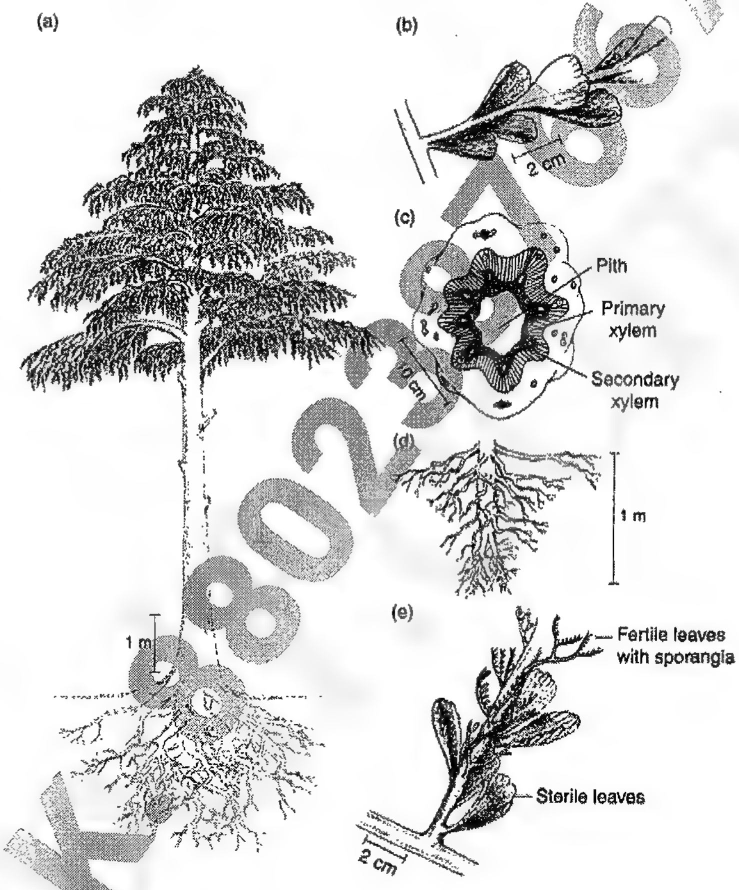

Figure 1. *Archaeopteris* tree: (a) habit; (b) leaves; (c) stem; (d) rooting system; (e) branch with sporangia and leaves

g. The wood was pycnoxylic that is characteristic of conifers.

h. Root penetration depths in excess of 1 m have been reported for this tree. Moreover, its root exhibited perennial root growth and the repeated production of lateral rootlets. The enhanced penetration of soils by its root system appears to have had a significant impact on pedogenesis (the development of soils) during the Late Devonian. Prior to the arrival of *Archaeopteris*, root systems rarely went deeper than 10 to 20 cm.

i. The stelar anatomy of *Archaeopteris macilenta* reveals eustelic condition. It also shows that the mesarch primary xylem is nine ribbed. A study by Scheckler (1978) has revealed that branches of *Archaeopteris* are protostelic at the base and become eustelic distally.

j. Branch and leaf traces diverge from these nine ribs - two of them give rise to branch traces and the remaining seven to leaf traces. All the traces are spirally arranged.

k. Secondary xylem was abundantly produced. It is compact and, in appearance, and typically coniferophytic. It comprises only tracheids and vascular rays.

Evolutionary relations of Progymnosperms

- Regarding Progymnosperms, a consensus has emerged in recent years that Gymnosperms could be of monophyletic origin having a common ancestry derived from a plexus of Progymnosperms.
- It is believed that both Cycadophytes and Coniferophytes have evolved from Progymnosperms.
- Among the Progymnosperms, Aneurophytes are considered older because they are protostelic throughout with three-dimensional dichotomous branching and terminal sporangia.
- The Aneurophytales have given rise to the Archaeopteridales and Cycadophytes.
- Archaeopteridales, in turn, gave rise to Coniferophytes.
- The protostele has given rise to eustele as seen in Archaeopteridales, Cycadophytes and Coniferophytes.

EXTINCT TAXA OF GYMNOPSERMS

PTERIDOSPERMS

General account of Cycadofilicales (Pteridosperms)

The Pteridosperms were the earliest gymnosperms. They constituted a very large and diverse assemblage of primitive seed plants.

They first appeared in Upper Devonian times and extended through the Carboniferous and Permian to the Mesozoic.

British palaeobotanists, F. W. Oliver and D. H. Scott, in 1904, established the concept of Pteridosperms (seed ferns) based on the detailed work on *Lyginopteris oldhamia* plant.

The pteridosperms showed the following diagnostic characters:

1. Formation of seeds
2. Leaves mostly large and fern-like, often many times pinnate.
3. Slender but woody stems.
4. Primary xylem mesarch (rarely exarch) in the form of protostele or primitive eustele
5. Secondary wood limited in amount, manoxylic and composed of tracheids with multiseriate pitting, especially on the radial walls.
6. Ovule and seed borne either on the frond or on a specially modified frond (megasporophyll)
7. No cone formation

Evolutionary time scale

The Pteridosperms first appeared in the Upper Devonian, had climax during the Carboniferous to Triassic and became extinct in the Cretaceous.

Due to their wide span of existence, they are divided into two broad groups:

1. Palaeozoic Pteridosperms (Upper Devonian to Permian)
2. Mesozoic Pteridosperms (Triassic to Cretaceous).

Salient features

1. The pteridosperms are the oldest seed plants. The oldest known seed plant species are *Elkinsia polymorpha* and *Archaeosperma arnoldii*.
2. They are also called seed-ferns because although they had fern-like foliage, and they reproduced by seeds.

3. Some members had a prostrate vine-like habit, but most were trees and similar in general appearance to modern tree ferns. The largest seed ferns in the fossil record were in the Medullosaceae family with forms up to 10 m in height.
4. Massive fern-like leaves were arranged helically on stem.
5. Primary xylem was mesarch (rarely exarch) with variable stelar configurations, ranging from simple protostele to eusteles.
6. Wood was manoxylic and limited in amount.
7. Thin-walled tracheids are with multiseriate pitting on radial walls.
8. Both pollen-bearing organs and ovules (seeds) were borne on leaves.
9. Pollen organs aggregated into clusters or arranged into large synangiate (fused) organs.
10. Seeds were large and solitary. The seeds were surrounded by a loose cupule. This small cup-like structure was lobed in the earliest seeds

Diversity

There is fossil evidence for at least eight families of seed ferns.

Family 1 :	Calamopityaceae (U. Devonian to L. Carboniferous)
Family 2 :	Lyginopteridaceae (Carboniferous)
Family 3 :	Medullosaceae (Carboniferous to Permian)
Family 4 :	Callistophytaceae (U. Carboniferous to Permian)
Family 5 :	Glossopteridaceae (U. Carboniferous to Triassic)
Family 6 :	Caytoniaceae (Triassic to Cretaceous)
Family 7 :	Peltaspermaceae (U. Permian to Triassic)
Family 8 :	Corystospermaceae (Triassic).

Fossil type study

One of the predominant genera of Pteridospernms was *Medullosa noei* (Figure 1) of the family Medullosaceae. The features of *Medullosa* tree are as follows.

1. *Medullosa* trees (e.g. *Medullosa noei)* grew to up to 10 m in height.
2. They had a wide-based stem with diameters of up to 0.5 m.
3. On the external part of the stem, the lower portion was covered with adventitious roots, whereas higher up there were spirally arranged leaf bases.
4. The adventitious roots provided support. Fossil evidence suggests that these roots could be up to 2.5 cm in diameter, and were abundant, with secondary tissues.

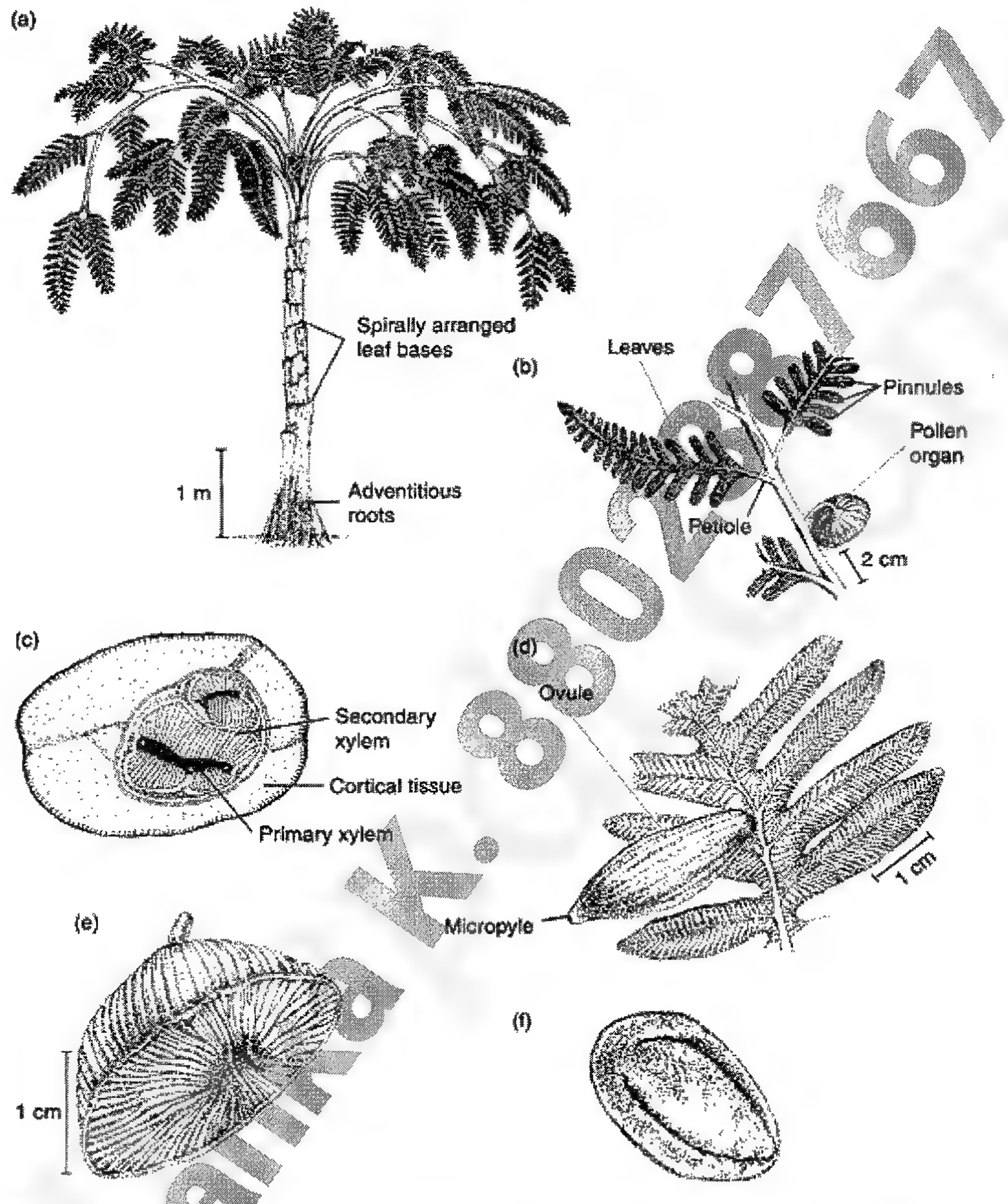

Figure 1: ***Medullosa noei*** **tree: (a) habit; (b) leaves; (c) stem and stelar structure; (d) ovules; (e) pollen organ; (f) pollen**

5. *Medullosa* had a complex stelar structure composed of a single stele divided into many vascular segments. Each vascular segment was made up of a central core of primary xylem, parenchyma cells and secondary xylem. The secondary xylem contained very large tracheids.

6. The secondary xylem was formed towards the inside of the primary xylem, unlike the situation in living plants.

7. The leaves of *Medullosa* were large megaphyllous fronds, pinnately divided and dichotomously branched. They were usually spirally arranged on the stem. Individual pinnules were usually approximately 2-4 cm in length.

8. *Medullosa* ovules are common in the fossil record and at least 14 morphologically distinctive types have been recognized. They range in size between 1 and 11 cm and have a three-layered enclosed integument with a micropyle and simple pollen chamber. These ovules share a close morphological similarity to cycad ovules, supporting the suggestion that the two are closely related.

9. The pollen grains of the *Medullosa* trees were located in pollen organs borne on fertile branches in clusters. These were large structures (2-3 cm in diameter) resulting from numerous fused sporangia.

CYCADEOIDALES (BENNETTITALES)

General Account

Also called **Bennettitales,** the Cycadeoides (belonging to **Cycadeoidales**) constitute an extinct order of gymnosperms which formed a significant part of land vegetation during the Triassic, Jurassic, and Cretaceous periods.

No known relatives of the Cycadeoidales exist at the present time, although members of the order Cycadales show some resemblances to the extinct group.

Due to certain features in common with cycads (order Cycadales), the members of Cycadeoidales are grouped with them and the seed ferns (order Pteridospermales) in the division Cycadophyta.

Both the cycadeoids and the cycads dominated the vegetation in middle Mesozoic times (about 150 million years ago)—called the "Age of Cycads"—and *both are presumed to have originated from the Pteridosperms*. The group became extinct toward the end of the Cretaceous.

Salient Features of Cycadeoidales

Cycadeoidales (Bennettitales) are characterized by leaf forms, which are similar to Cycadales in form, structure and venation. The main difference is the presence of syndetocheilic stomata in cycadeoids and haplocheilic stomata in cycads. Some of the general characteristics of this group are:

1. Stem always woody, stout or slender, undivided or forking, bearing large compound (rarely simple)

2. Columnar trunks (Williamsoniaceae and Wielandiellaceae); nearly 2 m in height or short tuberous branched or unbranched spherical or conical or irregular trunk up to 50 cm in diameter (Cycadeoidaceae)

3. Surface covered with rhomboidal leaf bases with or without hairs (ramenta) in between

4. A crown of pinnately compound leaves present at the apex.

5. Leaves with parallel venation and syndetocheilic stomata.

6. Reproductive structures in uni-/or bisexual cones or 'flowers' protected by many bracts

7. Numerous stalked or sessile ovules on conical, cylindrical or dome shaped receptacle
8. Ovules interspersed with interseminal scales with their distal ends fused to form a shield through which micropyles protrude
9. Microsporophylls in whorls, free or united, pinnate or entire with numerous microsporangia usually fused in a synangium or 'capsules';
10. Pollen grains monocolpate (*Colpus* is an oblong to elliptic germinal aperture in a pollen and a *monocolpate* pollen is a pollen grain having one colpus, as is commonly found in most petaloid monocotyledon species)
11. Embryo dicotyledonous.

Diversity

The order Cycadeoidales has been classified into three families viz.,

1. **Williamsoniaceae:** which have slender, branching trunks and either bisporangiate or monosporangiate strobili.
2. **Wielandiellaceae:** with slender, dichotomously branched trunk with simple, petiolate and lanceolate leaves.
3. **Cycadeoidaceae**: with stout trunks and bisporangiate reproductive structures.

Some authors have preferred to merge Wielandiellaceae into Williamsoniaceae.

Fossil type study 1: *Williamsonia*

The members of Wiiliamsoniaceae are characterized by slender, branching trunks and either bisporangiate or monosporangiate strobili.

Williamsonia, the best-known genus of its family, had a columnar trunk with frondlike leaves at branch tips; its fossil cones are not well defined.

They have been described from many sites in different regions of the world including India. In India five species were discovered from Rajmahal Hills in Jharkhand viz., *W. indica, W. microps, W. sahnii, W. santalensis* and *W. sewardiana.*

The plant *W. sewardiana* was reconstructed by Sahni (1932) on his studies of the material of Jurassic period collected from Rajmahal Hills. It was the first reconstruction of a fossil plant from India.

Figure 2: ***Williamsonia*** **tree**

1. It consists of a columnar stem, about 2m long with prominent spirally arranged rhomboidal leaf bases and a crown of unipinnately compound leaves.
2. Stems are simple or monopodially or dichotomously branched.

3. Two types of branches have been described:
    a. the sterile or vegetative shoots, and
    b. the fertile shoots which terminate in a 'flower' or cone.
4. Only pinnately compound foliage leaves are present on lateral shoots. The main shoot bears, in addition, small scale like pointed leaves.
5. The lateral shoots show a prominent constriction at the base. It is presumed that they get detached and serve as a means for vegetative propagation.
6. The stem shows a wavy, rough outline due to the presence of numerous leaf bases. A wide parenchymatous cortex encircles a narrow pith. Both the cortex and the pith contain secretory ducts.
7. The conjoint, collateral and endarch vascular bundles are embedded in pith. A distinct cambium is present.
8. The secondary wood is manoxylic.
9. The reproductive fructifications of Williamsoniaceae, studied so far, are unisexual.
10. The plants of Williamsonia were found to be dioecious.
11. The The male fructifications were never found in actual connection with the plant, and are referred to the genus *Weltrchia*.
12. The microsporophylls are arranged in a whorl.
13. Seed-bearing organs have been described under different genera. They developed on lateral shoots arising from the axil of a leaf. These shoots bear both scale and foliage leaves, and a terminal cone.
14. The female cones of *W. sewardiana*, *W. harrisiana* and *W. gigas* consist of a well developed central conical receptacle bearing stalked ovules and interseminal scales in a spiral manner.
15. The mature seeds of *Williamsonia* have been studied by Sharma (1970). They are stalked, dicotyledonous and endospermic.

Fossil type study 2: *Cycadeoida*

Cycadeoidea is probably the only genus of the family Cycadeoidaceae, distributed from Upper Jurassic to Upper Cretaceous, comprising about thirty species.

The majority of the species are found as petrified trunks from America and a few from Europe, and India.

Cycadeoidea had ovoid or short columnar trunks which are unbranched or sparsely branched.

The trunks were massive, about 1 m in length and about 60 cm in diameter. The surface of the stem was covered with prominent rhomboidal leaf bases and multicellular hairs in between them.

The short stout trunks are much different from the members of Williamsoniaceae and Wielandiellaceae.

The anatomical details have been well worked out in *Cycadeoidea*. A cross-section of the trunk shows large parenchymatous pith surrounded by a thin zone of primary wood with endarch protoxylem and secondary wood with scalariform tracheids. The wood was typically manoxylic.

The mature leaves in Cycadeoidea have not been found attached to the trunks. It is, however, assumed on good evidence that leaves were borne in a crown at the apex of the trunk.

The reproductive fructifications (flowers) of the cycadeoidean members were axillary in position (in the axil of leaf bases). The flowers were bisexual in *Cycadeoidea*. These were borne on a small pedicel and were protected by about 100 spirally arranged, pinnate bracts covered by scales. The bracts opened up at maturity to form a broad saucer-shaped structure.

The pollen bearing organ consisted of about twenty pinnate microsporophylls arranged in a whorl at the base of ovuliferous receptacle.

Numerous tiny, stalked orthotropous ovules, about 1 mm long, were present in a cluster at the conical or dome-shaped apex of the fertile shoot. They were interspersed with interseminal scales which were about same in number as the ovules. Their heads were enlarged into a club which became fused with the adjoining interseminal scales in a way that it formed a continuous surface layer with openings through which micropyles projected. This continuous surface layer constituted an external protective covering (or pericarp) over the developing seeds. .

At one point, the Cycadeoidales were put forward as possible flowering plant ancestors because of their flower-like bisexual reproductive structures. In *Cycadeoidea*, ovules alternated with interseminal scales on an ovulate receptacle at the center of several organ whorls. This reminded some workers of the angiosperm carpel.

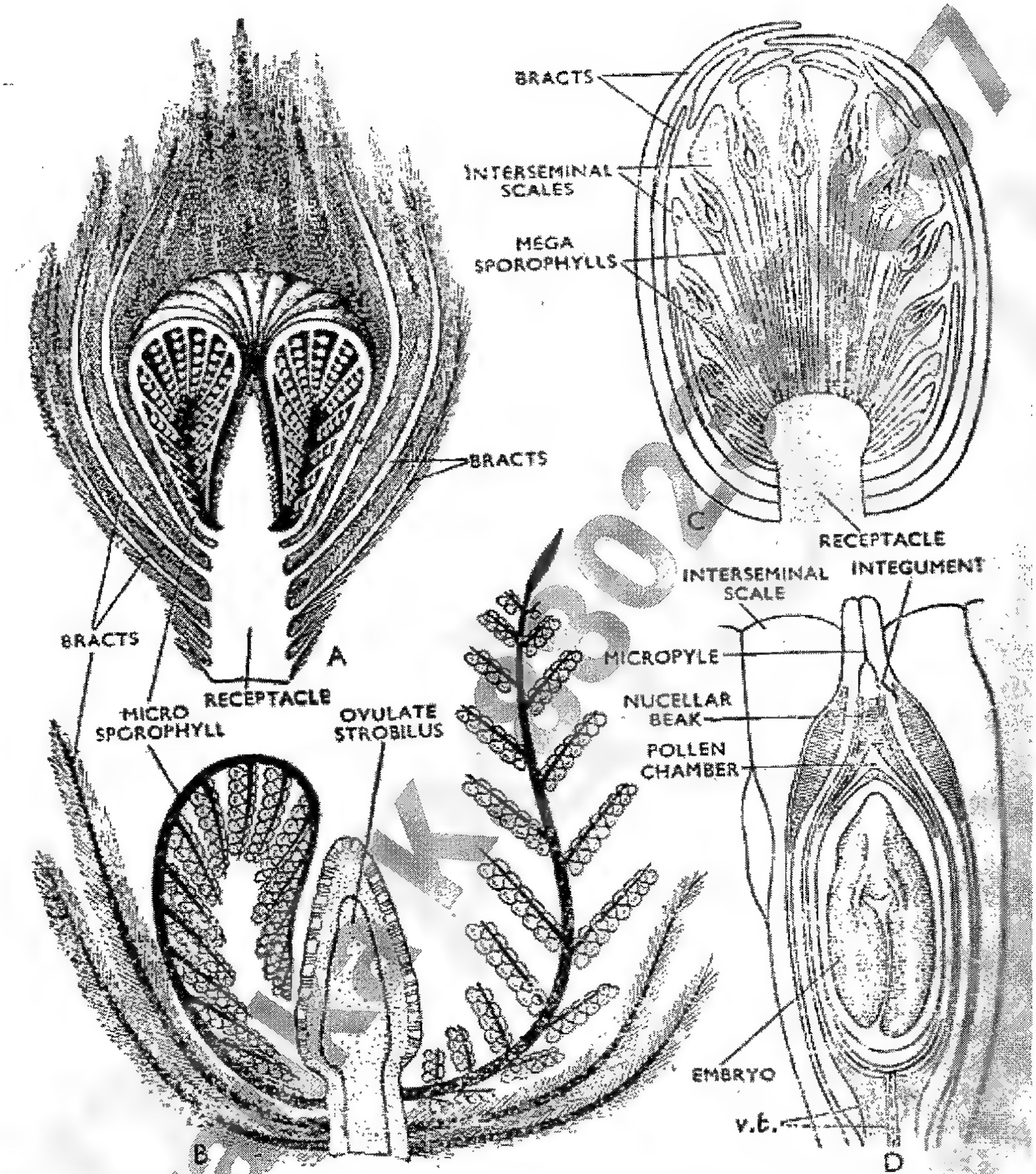

Figure 3: The details of *Cycadeoidea* "flower": A. Unexpanded flower B. Same with a microsporophyll expanded. C. A mature fruit each ovule showing a dicotyledonous embryoD. Vertical LS of seed

Relationships with Other Groups

Cycadeoidales, as a group, reflects similarities (and differences too) with many groups but the reproductive structures specially those having stalked ovules are unique.

Cycadeoidales and Cycadales

Both the groups exhibit similar habit and morphologically similar fronds. Histologically, the stems are similar having manoxylic wood. They have monocolpate pollen grains, orthotropous ovules and dicotyledonous embryo. Some of the major differences between the two groups are different anatomical details of the frond; haplocheilic stomata in Cycadales and syndetocheilic in Cycadeoidales; girdling leaf traces which are prominently displayed in a cycad stem are absent in the members of Cycadeoidales. Based on these differences, Andrews (1961) opined that both the groups have evolved along two different and independent lines.

Cycadeoidales and Pteridospermales

The two groups share a large number of characters such as presence of ramental hairs, similar internal structure, syndetocheilic stomata, direct leaf traces, presence of leafy microsporophyll bearing synangia and the presence of cupule. The bisporanglate flower of Cycadeoidales could be compared to bisporangiate fronds of Cycadofilicales (Pteridosperms). According to some authors, there are two lines in the course of evolution from Cycadofilicales. Of these, one gave rise to monosporangiate forms like Cycads, and the other to Cycadeoidales, which has both mono- and bisporangiate forms.

Cycadeoidales and Angiosperms

The similarity in 'strobili' or 'flower' of Cycadeoidales and the flowers of some angiospermous groups (such a Ranales and Magnoliales which have primitive flowers with numerous floral parts arranged spirally) lead a few morphologists (Bessey, Hallier, Hutchinson, etc.) to believe that the angiosperms might have originated from mesozoic Cycadeoidales. Some of the other similar characters are the spirally arranged hairy bracts around reproductive organs in Cycadeoidales which could be compared to the perianth of angiosperm; the mesoparacytic stomata of Magnoliales and the syndetocheilic stomata of Cycadeoidales; homoxylous (without vessels) wood comparable to few angiosperms like *Drymis*. It is currently established that the flowering plants arose in the early Cretaceous (120-130 mya); however, no fossils showing a transition from gymnosperm to angiosperm have been discovered. This makes the origin of the angiosperms mysterious.

CORDAITALES

General account of Cordaitales

In an outline classification of the conifers, K.R. Sporne has identified 4 orders [1965], namely:

1. Cordaitales [a fossil group]
2. Gingkoales
3. Taxales
4. Coniferales

The Cordaitales – also called Cordaites (After A.J. Cords, Australian botainst) represent an extinct group of primitive gymnosperms. **They were the earliest known cone-producing seed plants**. They **first appeared in the late Devonian** and were very abundant in the Mississipian, Pennsylvanian and Permian periods, but probably became extinct in the early Mesozoic Era.

It is now widely accepted that **cordaitalean gymnosperms represent the ancestral group to the modern day conifers**.

The Cordaitales have arisen from advanced progymnosperms like *Archaeopteris* of the Devonian period.

Salient features of Cordaitales

1. All evidence obtained so far suggests that the cordaites were predominantly trees and occupied a range of different habitats from mangrove-type habitats to drier uplands (Cleal and Thomas, 1999).
2. With fossil trunks measuring up to 30 m in height and 1m in diameter, these plants may have represented some of the tallest trees in the late Carboniferous and Permian forests. *Cordaites* and *Dorcordaites* were very tall trees probably the tallest in the carboniferous forests.
3. Trees in the cordaites group all had a main stem with single branches radiating out towards the top of the axis.
4. The stem showed an eustele, with large pith, a thick or thin vascular cylinder, and a small cortex.
5. Unlike the mesarch and collateral bundles of the Cycadofilicales, those of the Cordaitales were endarch and collateral.
6. The tracheids bore circular, bordered pits in more than 2 to 5 rows, as in *Araucaria,* a modern conifer genus.
7. The leaf traces were double, collateral and endarch but became mesarch on entering the petiole.
8. In cross-section the trunk was composed of large amounts of secondary xylem surrounding a narrowly medullated primary stele (pycnoxylic wood).
9. Cordaitean leaves were variable, but usually helically arranged on long, slender branches. Many species in the fossil record bear a close morphological similarity to leaves of the exant genus *Agathis* (Araucariaceae).
10. The leaves themselves were strap-shaped or tongue-shaped, and up to 1 m in length and 15 cm in width.
11. The tip of the leaf was bluntly rounded with a broad leaf base attaching it to the branch.
12. Rooting systems of the cordaites were variable in structure. Fossil evidence suggests that some groups had extensive rooting systems, with lateral roots radiating from large branched primary roots.
13. Reproductive structures were borne on the same branches as the leaves. They were monosporangiate *i e.*, they were staminate or ovulate.

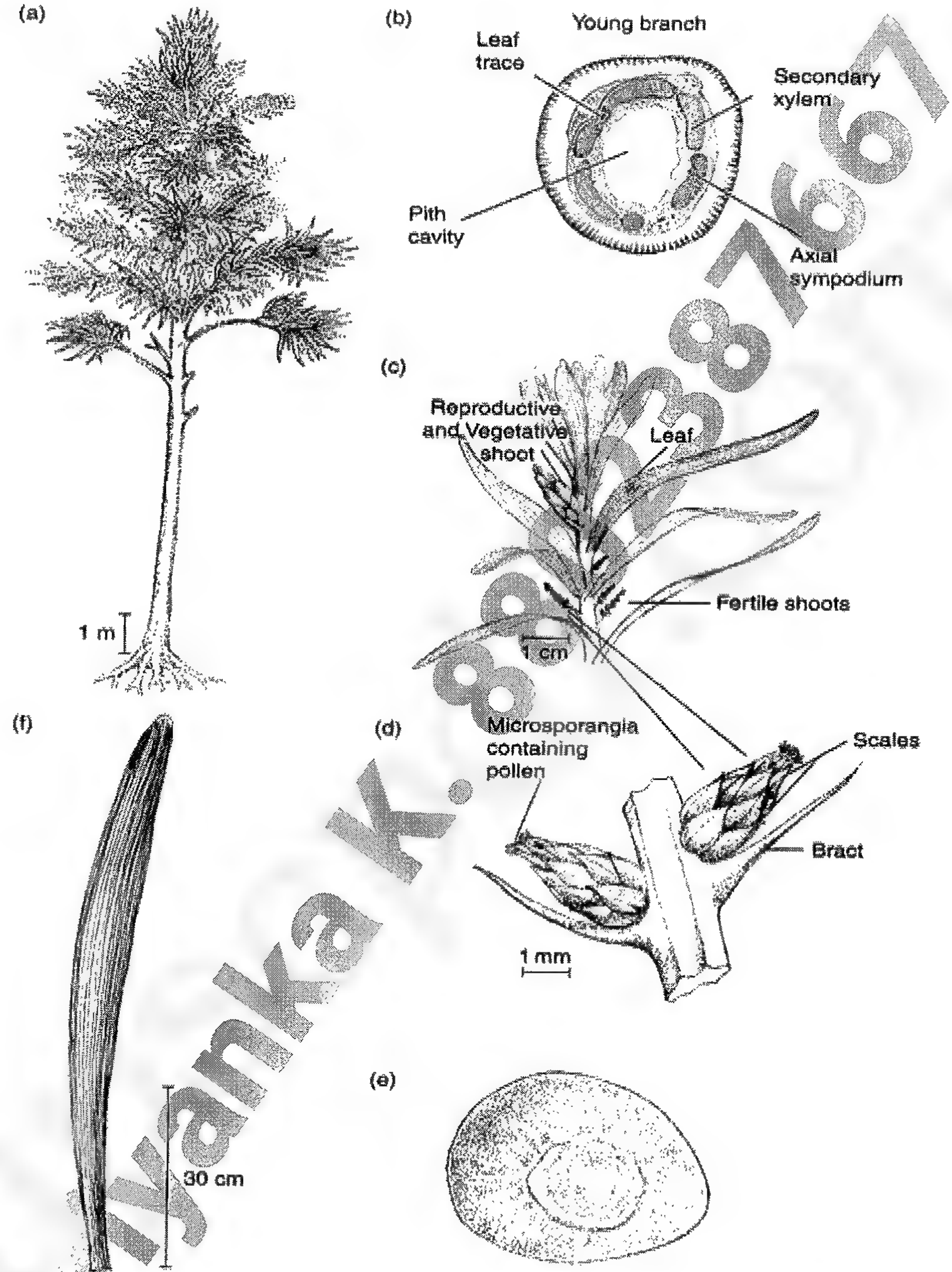

Figure 4: Cordaitales tree: (a) habit; (b) stem stelar structure; (c) branch with leaves and reproductive shoots; (d) reproductive structures; (e) pollen (45-65μm in diameter); (f) leaf

14. Male and female organs were thus separate but probably located on the same tree (Bell, 1992).

15. The strobili of *Cordaites* have been given separate generic name *Cordianthus* since their fossils have not been found attached to the *Cordaites* tree. They were borne as small budlike structures in the axils of bracts.
16. The male organs were located on shoots up to 1 cm long that contained a number of scales arranged around the shoot axis in a spiral, forming a structure similar to a conifer cone.
17. The female reproductive organs were also located on the branches and bore some similarity to the male organs in that they were cone-shaped and composed of fertile and infertile scales. However, in the female organs, the fertile scales terminated in ovules.
18. The ovule bears a striking resemblance to that of the *Ginkgo*. The integument had an outer fleshy and middle stony layer, but no inner fleshy layer. Nucellus was entirely free from the integument
19. The gametopbytes were reduced. The pollen grains are preserved in large quantities. Nucellar beak and pollen-chamber were prominent, thus indicating the presence of swimming sperms.
20. Each seed was surrounded by three integumentary layers, forming an enclosed seed coat with micropyle. The margin of the seed extended as a wing (platyspermic).

CYCADS

Introduction to the Cycads

The extant gymnosperms are probably a clade, although that has not been established beyond a doubt. The gymnosperms are seed plants that do not form flowers. Gymnosperms derive their name (which means "nakedseeded") from the fact that their ovules and seeds are not protected by ovary or fruit tissue. Although there are probably fewer than 850 species of living gymnosperms, these plants are second only to the angiosperms in their dominance of the terrestrial environment.

The four major groups of living gymnosperms bear little superficial resemblance to one another:

1. The cycads (*Cycadophyta*) are palmlike plants of the tropics and subtropics, growing as tall as 20 meters. Of the present-day gymnosperms, the cycads are probably the earliest-diverging clade. There are 140 species of cycads. Their tissues are often highly toxic to humans.
2. Ginkgos (*Ginkgophyta*), which were common during the Mesozoic era, are represented today by a single genus and species, *Ginkgo biloba*, the maidenhair tree. There are both male (microsporangiate) and female (megasporangiate) maidenhair trees. The difference is determined by X and Y sex chromosomes, as in humans and few other plants which have sex chromosomes.
3. Gnetophytes (*Gnetophyta*) number about 90 species in three very different genera, which share certain characteristics analogous to ones found in the angiosperms.
4. Conifers (*Coniferophyta*) are by far the most abundant of the gymnosperms. There are about 600 species of these cone-bearing plants, including the pines and redwoods.

Order Cycadales

The members of this order are commonly known as **cycads.** They originated from the seed ferns, i.e., Cycadofilicales, towards the end of the Carboniferous period and formed a dominant vegetation during the Triassic period of Mesozoic era. This period is also known as **'age of cycads'**. The order includes nine living genera and about 100 species. They are usually woody trees except ***Zamia pygmaea.*** The stem is mostly unbranched and is covered by persistent leaf bases. The stem is mostly unbranched and is covered by persisted leaf bases. The leaves are arranged in whorls at the apex of the stem; they are pinnately compound. The wood is manoxylic. The micro- and megasporophylls usually form male and female stobili (in *Cycas* the megasporophylls, however, do not form compact strobili). The male gametes are motile.

Genus: *Cycas*

General Introduction

Cycas is the most widely distributed genus of the order Cycadales. There are about 20 species distributed in Australia, Africa, Nepal, Bangladesh, Myanmar and India. Four species of Cycas – *C. circinalis, C. pectinata, C. rumphii and C. deddomei* – occur in natural state in India chiefly in Assam, Orissa, Meghalaya, Andaman and Nicobar Islands, Karantaka and Tamil Nadu. *C. revoluta and C. siamensis* are widely grown in gardens.

Species of *Cycas* are of considerable economic importance. Stems and seeds of several species are used for extracting starch. Young succulent leaves are often used as vegetable in some parts of India, Malaya, Philippines and Indonesia. Many species of *Cycas* are widely used in indigenous systems of medicine for the treatment of various ailments. The juice of young leaves of *C. circinalis* is used as a remedy for disorders of stomach, flatulence, blood vomiting and skin diseases. A hair-wash prepared from the pounded and crushed stems of *C. pectinata* is used in Assam for the treatment of diseased hair roots. Pollen grains of some species of *Cycas* are strongly narcotic, and microsporophylls of C. *rumphiii and C. circinalis* are used as anodynes. A gum obtained from *C. rumphii* is effective in healing malignant abscesses. Leaves of C. *revoluta* are rich in nitrogen and they are used as green manure for rice, sweet potato and sugarcane.

Sporophyte Structure

Cycas is an evergreen slow-growing palm-like small tree with an average height of 1.5 - 4 m, commonly found in xerophytic habitats, such as exposed slopes of hills and other sunny places where water is scarce. It also grows well under cultivation in gardens.

The sporophytic plant body is differentiated into roots, stem and leaves.

Figure 1: *Cycas* **mature sporophyte**

Roots

There are two types of roots in *Cycas*: **normal tap roots** and **apogeotropic coralloid roots.**

(a) **Normal tap roots.** Long-lived primary root forms tap rot. The main taproot is usually thick and short but its lateral branches are thin long.

These roots are positively geotropic and their main function is anchorage and absorption of water and mineral nutrients.

(b) Coralloid roots. These are specialized apogeotropic roots which grow on the surface of the soil. They are repeatedly dichotomously branched and appear as coralline masses. A specific algal zone with colonies of *Anabaena or* other blue-green algae is present in the cortex of these roots. The algae perhaps helpful in nitrogen-fixation. The coralloid roots possess lenticels, which help in respiration.

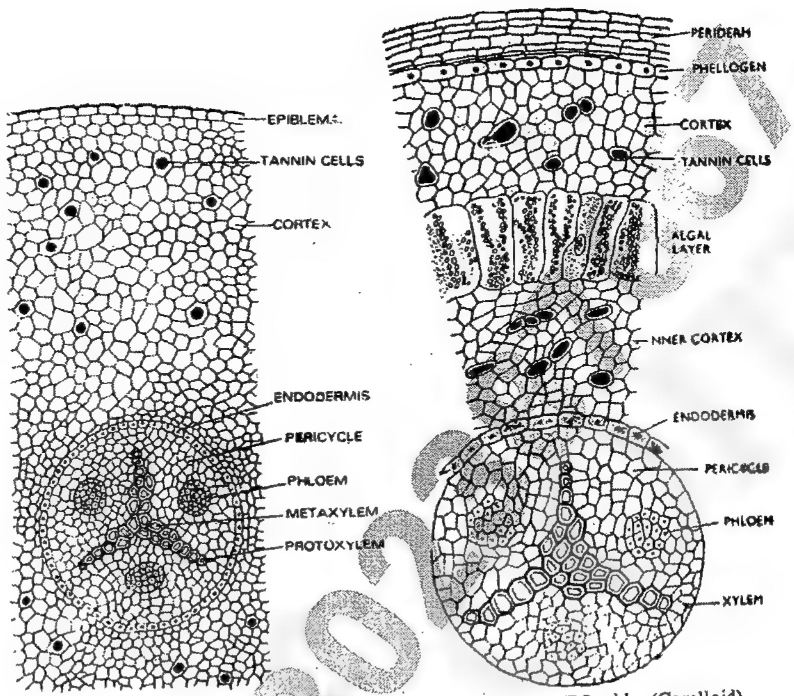

Figure 2: A. TS through Tap root. B. TS through coralloid root

Internal tissues of root are differentiated into **epiblema, cortex and central vascular tissue**.

Epiblema is composed of a single layer of thin walled cells. Some cells of epiblema give rise to hairs.

Cortex is a multilayered zone of thin-walled parenchymatous cells which are filled with starch. Some tannin cells and mucilage cells are also present this region. The innermost layer of the cortex forms endodermis. The endodermal cells are characterized by the presence of casparian bands.

Pericycle is multi-layered and consists of parenchymatous cells.

Vascular tissue form a central **triarch** stele. The xylem is exarch and tracheids of the protoxylem have spiral thickenings and those of the metaxylem sclariform thickenings. The pith is reduced or completely absent.

The mature normal root shows secondary growth which starts by the formation of cambium strips inner to the primary phloem strands. These cambium strips cut off secondary phloem towards the outer side and secondary xylem towards the inner side. Due to the pressure of secondary tissues, the primary phloem is crushed but the primary xylem can be seen in the center of the stele. A distinct layer of phellogen or cork cambium arises in the outer region of the cortex which gives rise to cork on its outer side and phelloderm or secondary cortex on its inner side. Cork, phellogen and phelloderm are collectively known as periderm. Due to the development of periderm, epiblema is ruptured.

The internal structure of coralloid roots is similar to that of normal roots. However, in coralloid roots cortex is differentiated into three distinct regions: (i) **outer cortex,** composed of compact polygonal cells, (ii) **inner cortex** and [iii] **Middle cortex** which forms algal zone. The algal zone consists of a single layer of loosely connected thin walled and radially elongated cells. In the algal zone blue-green algae, such as *Anabaena, Nostoc* and *Oscillatoria* occur which live symbiotically. Besides, some fungi and bacteria (e.g *Pseudomonas, Azotobacter)* are also found in this zone. Development of the algal zone takes place after the entrance of endophytic algae. According to some investigators, presence of algal zone is not universal character of coralloid roots. Coralloid roots show little or no secondary growth.

Stem

The young stem is tuberous and subterranean and its apical part remains covered with brown scale leaves. In older plants, the stem becomes thick, columnar and woody. It is covered with persistent and woody leaf bases. The stem is usually unbranched, but sometimes due to injury shoot apical meristem is divided into two parts and the stem appears as dichotomously branched.

The stem is irregular in anatomical outline due to the presence of numerous persistent leaf bases. Its internal structure is similar to that of a dicotyledonous stem. It is differentiated into **epidermis, cortex and vascular cylinder.**

Epidermis is the outermost layer, covered with a thick cuticle. It is usually discontinuous due to the presence of persistent leaf bases.

Cortex forms the major part of the stem and it is composed of parenchymatous cells, rich in starch grains. The cortex is also traversed by several mucilaginous canals and many leaf traces. The inner wall of mucilaginous canals is made up of radially elongated secretory cells. The innermost layer of the cortex is endodermis and it is followed by pericycle. However, both endodermis and pericycle are indistinct. Numerous leaf traces can be seen in the cortical region. They are vascular strands that supply the leaves.

In the young stems, the **Vascular cylinder** is very small in comparison to the cortex. There are several vascular bundles arranged in a ring, forming an **ectophloic eustele**. The vascular bundles are conjoint, collateral, endarch and open. The individual bundles are separated by parenchymatous medullary rays. The xylem is composed of tracheids and xylem parenchyma only; vessels are absent. The tracheids of protoxylem have spiral thickenings, whereas

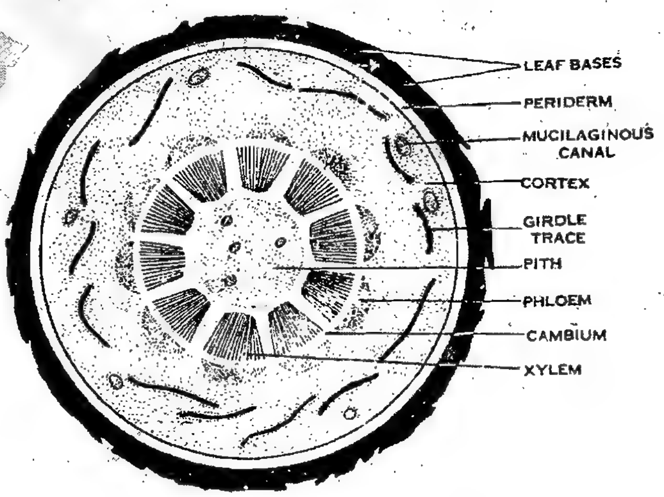

Figure 3: TS through the primary stem

those of metaxylem, scalariform thickenings. The phloem is composed of sieve tubes and phloem parenchyma; companion cells are absent.

Leaf Traces: Each leaf receives four leaf traces. Of these, two arise on the same side as the leaf any they enter directly into the leaf. These traces are known as **direct traces.** The other two arise opposite the leaf and enter the leaf after turning around the vascular cylinder. These traces as such form a girdle around the vascular cylinder, hence they are called **girdle traces.** Before entering the rachis, all the four leaf traces divide to form several strands and hence there are several vascular bundles in the rachis.

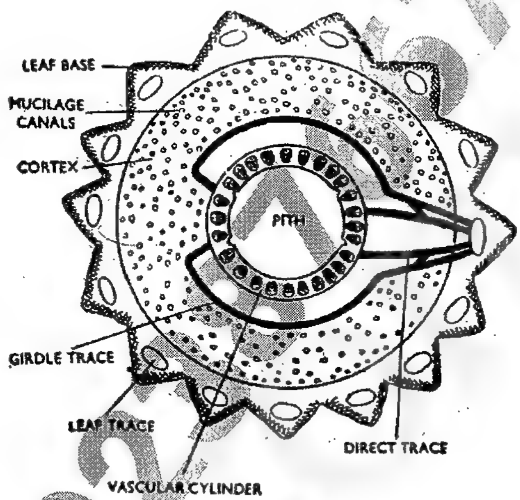

Figure 4: Origin of leaf traces

There is a parenchymatous **pith** in the center of the stem. The pith cells are rich in starch, and several pith cells also contain tannins and mucilaginous substances.

The stem of *Cycas* shows normal secondary growth in early stages, similar to that of a dicotyledonous stem. Interfascicular cambium strips develop between the two vascular bundles and join with intrafascicular cambium strips and as such a complete ring of cambium is formed. This cambial ring cuts off secondary xylem on the inner side and secondary phloem on the outer side. Multiseriate bordered pits are present on the walls of the secondary xylem.

In addition to secondary vascular tissue, the cambium also forms well developed parenchymatous medullary rays. Hence the wood is **mannoxylic**.

The cambial ring remains functional only for a short time and thereafter its activity ceases. It is succeeded by another cambium, formed independently in the pericycle or the inner layers of the cortex. The new cambium like old cambium forms secondary xylem towards the inner side and secondary phloem towards the outer side. This cambium also becomes inactive after sometimes, and is superceded by another cambial ring form din a similar fashion. In *C. pectinata,* as many as 20 rings of cambium may be formed. Thus **at maturity *Cycas* stem is polycyclic.**

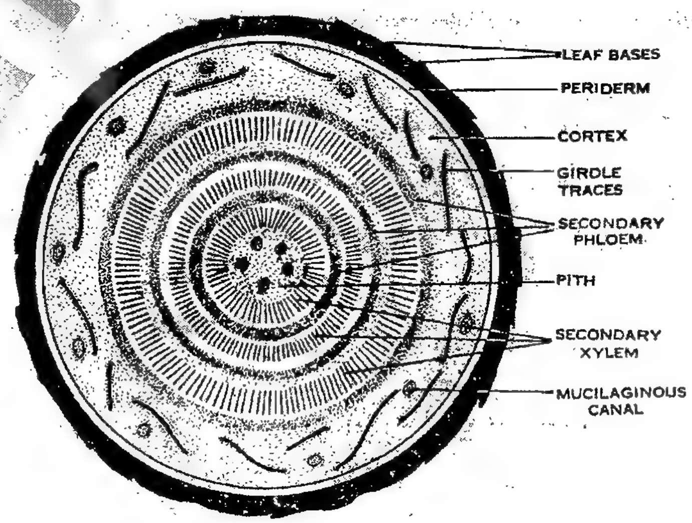

Figure 5: Polycyclic wood in *Cycas*

Extrastelar secondary growth takes place by the formation of phellogen (cork cambium), which forms phelloderm (secondary cortex) on the inner side and phellem (cork) on the outer side.

Leaves

Cycas has dimorphic leaves, which are arranged in close alternate whorls at the apex of the stem.

Foliage or assimilatory leaves: Larger, pinnately compound foliage leaves form a crown at the top of the stem. Usually a single crown of leaves is formed in a year but in some species (e.g., *C. rumphiii, C. circinalis)* two crowns are formed in a year. Each leaf has 80-100 pairs of leaflets which are arranged on both sides of the rachis in opposite or alternate manner. The leaflaets are sessile, elongated and ovate or lanceolate. The rachis of a very young leaf is circinate with circinately coiled leaflets like those of ferns. The young leaves are covered with ramenta.

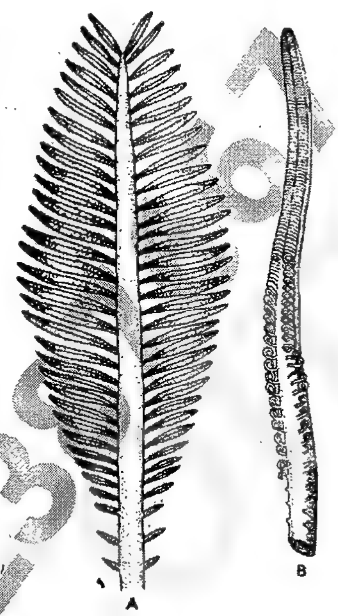

Figure 6: *Cycas* leaf

Scale leaves: The scale leaves are small, rough, dry and triangular. They are thickly covered with ramenta. They are incapable of carbon assimilation and their main function is the protect apical meristem and other aerial parts. The scale leaves also have persistent leaf bases which from part of the armour of the old stem.

Reproduction

Cycas reproduces by **vegetative and sexual** means.

Vegetative Reproduction

Vegetative propagation takes place by **adventitious buds or bulbils.** They develop in the basal part of the stem from parenchymatous cells of the cortex in the crevices between persistent leaf bases. The base of the bulbil is covered with scale leaves. a few foliage leaves develop from its center.

It is a common method of propagation in *C. revoluta,* as male plants of this species usually do not occur in Northern India and in their absence sexual reproduction is not possible. Bulbils formed on male plants give rise to male plants and those developed on female plants form female plants.

In *C. circinalis,* vegetative propagation takes place by suckers which develop from the roots They grow horizontally in the ground for some distance and then form new plants.

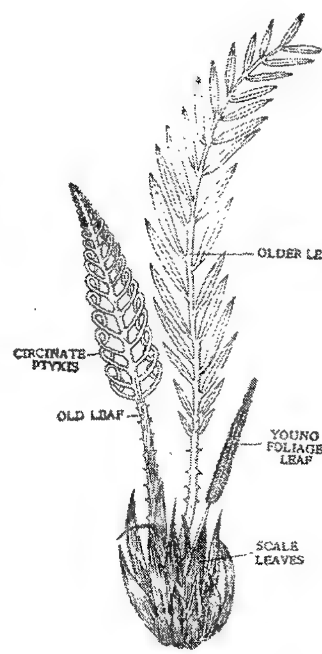

Figure 7: A bulbil

Sexual Reproduction

Cycas is a heterothallic plant; the male and female gametophytic phases develop from two different kinds of spores. The male gametophyte develops from microspore and the female from megaspore. The micro-and megaspores are formed in microsporangia and megasporangia respectively.

Species of *Cycas* are strictly **dioecious** and either male cones or megasporophylls ornformed on a given plant. In India, most of the plants of *C. circinalis* are male and those of *C. revoluta* are female.

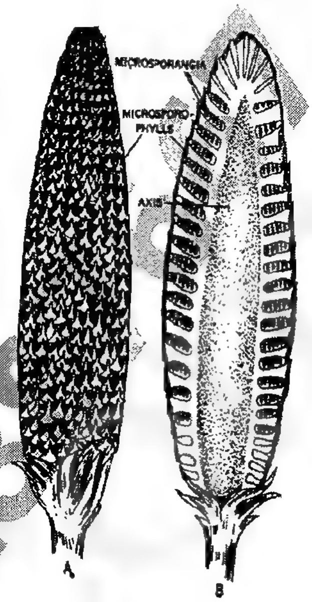

Figure 8: Male cone. A. External appearance B. Same in LS

Male strobilus. The male strobilus (cone) develops at the apex of the stem in between the crown of foliage leaves . In its development apical meristem of the stem is utilized and as a result the future stem becomes sympodial. The male cone is a shortly stalked, compact, oval or conical woody structure. It is 40-80 cm in length, perhaps the largest amongst the plant kingdom.

The male cone consists of several microsporophylls which are arranged spirally around a central cone axis. The microsporophyll is a woody, more or less flattened and nearly triangular structure. It is differentiated into a proximal wedge-shaped fertile part which expands distally form a narrow point of attachment and a distal sterile part, tapering into an upcurved apophysis. The upper (abaxial) surface of the fertile part of the microsporophyll is sterile, while on the lower (adaxial) surface there are 700-1,000 microsporangia, arranged in definte grounds, known as **sori**. There are 3-6 microsporangia in a sorus. Many delicate hairs are also present on the surface of the microsporophyll amongst on the surface of the microsporophyll amongst sporangia. They protect young sporangia and perhaps also help in dissemination of microspores.

The microsporangia are sessile or are attached to the lower surface of the microsporophyll by a very short stalk. The wall of the microsporangium is differentiated into three regions – an outer **exothecium,** consists of thick-walled and cutinized cells; a middle **endothecium,** made up of thin walled cells; and an inner nutritive **tapetum.** There are a very larger number of microspores in a sporangium.

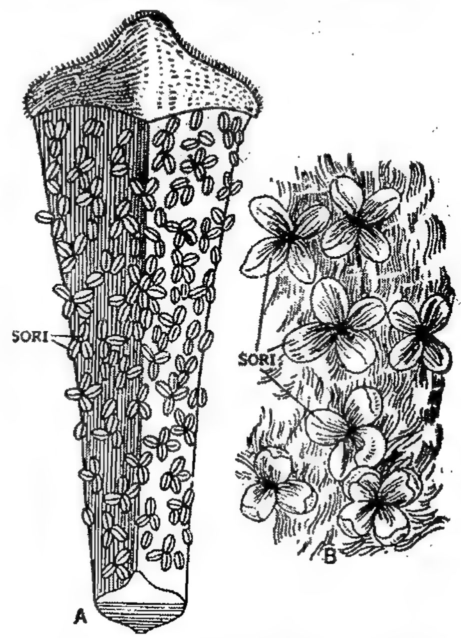

Figure 9: A. A microsporophyll lower surface B. Sori

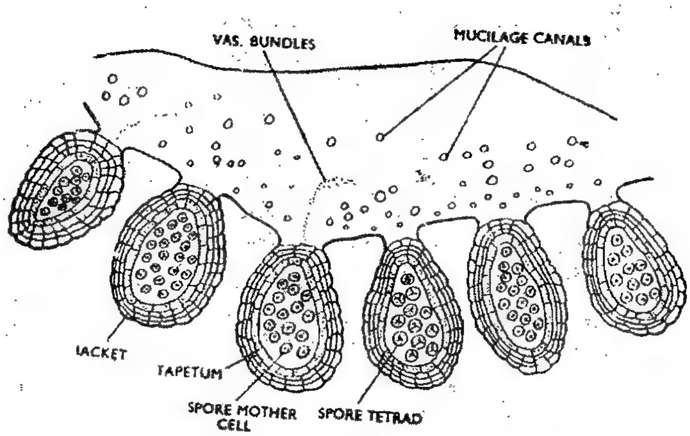

Figure 10: Microsporangia

With the maturation of microspores the axis of the male strobilus elongates. This results in separation of microsporophylls and the groups of sporangia present on their dorsal surface are thus exposed. The walls of the exposed sporangia dry up and break at the line of dehiscence thus releasing the microspores.

The microspores germinate within the sporangium before dissemination. Thus the male gametophyte develops partially inside the sporangium before pollination and partially within the pollen chamber of the ovule after pollination. The development of the male gametophyte before pollination takes place inside the microsporangium. The microspore divides by a transverse wall into two unequal cells, a small **prothallial cell** and a large **antheridial cell**. The prothallial cell does not divide further. The antheridial cell divides to form a small **generative cell** (adjacent to the prothallil cell) and a large **tube cell**. Thus the microspore become 3- celled. The dispersal of microspores takes place at the 3-called stage.

Female reproductive structures. The megasporophylls of *Cycas* are not organized into cones and instead they occur in close spirals in acropetal succession around the stem apex of the female plant. New megasporophylls are produced every year like the foliage leaves. They are produced in larger numbers than the foliage leaves. The megasporophylls of a year occupy position between the successive whorls of foliage leaves. The growth of the apical meristem of the female plants is monopodial; the axis continues to grow as it produces foliage leaves and megasporophylls.

The megasporophylls are considered to be modified leaves. They are flat and dorsiventral structures, measuring 15-30 cm in length. A megasporophyll is differentiated into a basal stalk and an upper pinnate lamina. Ovules are formed on the lateral sides of the stalk. The number of ovules varies from 2-10, depending on the species. There is a great variation in the structure of megasporophylls in various species, as displayed below.

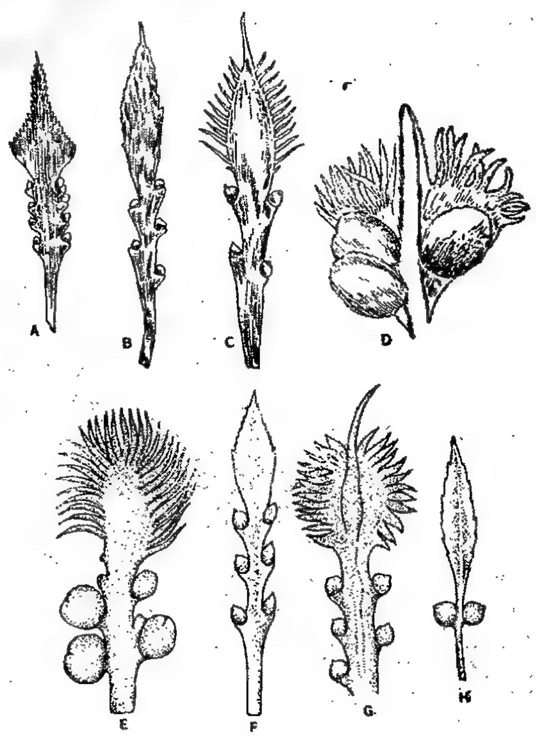

Figure 11: Many types of megasporophylls

The ovule of *Cycas* is orthotropous and unitegmic.

It is sessile or shortly stalked and perhaps largest in the plant kingdom; about 6 cm in length and 4 cm in diameter. The ovule consists of a large nucellus surrounded by a single integument. The integument remains fused with the body of the ovule except at the apex of the nucellus, where it forms a nucellar beak and micropyle.

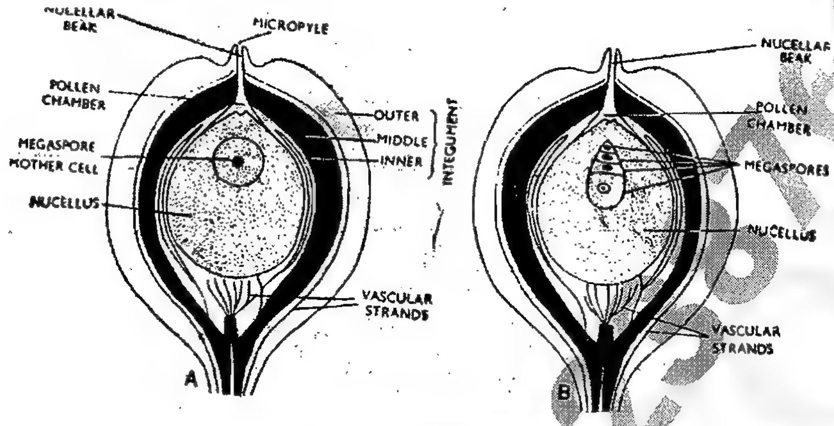

Figure 12: Ovule. A. Young B. Mature

The integument is very thick and is differentiated into three distinct layers- the outer and inner layers are fleshy, whereas the middle layer is hard and stony. The inner fleshy layer remains fused with the nucellus and it is short-lived.

In synchronzation with the time of dispersal of the microspores, some cells of the nucellar beak disorganise to from a viscuous fluid. This fluid oozes out from the microphyle in the form of a pollination drop. Some of the microspores, carried by air current, are entangled in the pollination drop. As the pollination drop dries up, the microspores are sucked into the pollen chamber through the micropylar canal. As the result of drying of the viscous fluid, the microphylar canal of the pollinated ovules is plugged. After pollination, the ovule increases in size. But unpollinated ovules dry up and wither away. The reproductive organs of some species of *Cycas* emit very penetrating odour at maturity.

Development of male gametophyte after pollination. Further development of the 3- called male gametophyte takes place within a week of pollination in the pollen chamber of the ovule. The generative cell divides to form a **stalk cell** and a **body cell**. About the same time, the exine ruptures and the intine protrudes out in the form of a pollen tube. The pollen tube penetrates the nucellar tissue and grows towards he female gemetophyte. In *Cycas*, has pollen tube is not only a sperm carrier but it is also haustorial in nature.

The stalk cell does not divide, whereas the body cell divides to form two male gametes (antherozoids) just before fertilization. The antherozoids swim freely in the cytoplasm of the pollen tube. There is an interval of about four months between the pollination and fertilization.

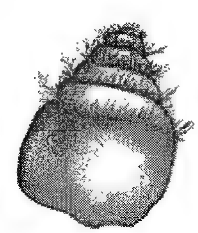

Figure 13: A sperm

The male gametes are naked, top-shaped structures, measuring 180-210 µm. The blepharoplast of the antherozoids elongates into a large spirally arranged structure with may cilia. The cycad sperm is the largest and most complicated motile cell in either plants or animals.

Female gametophyte: The female gametophyte develops from the functional megaspore which is deeply situated in the ovule. The nucleus of the megaspore divides by free nuclear divisions to form a large number of nuclei. Simultaneously, the megaspore also increases in size. A vacuole develops in the center of the megaspore which forces the cytoplasm towards the periphery. Formation of cell wall starts from the periphery and extends towards the center. The wall formation is a very rapid process and the entire gametophyte becomes cellular shortly. The tissue thus formed is called **female prothallus or endosperm.** The cells of the endosperm are haploid. The nucellus is used up as the gametophyte develops and it is represented by a very thin layer in the mature gametophyte.

Development of archegonia. Some superficial cells of the female gametophyte at the micropylar end enlarge in size and functionas archegonial initials . An archegonial initial divides by a periclinal wall to form an outer **primary neck cell** and an inner **central cell**. The primary neck cell divides by a vertical wall and gives rise to two **neck cells.** These cells form the archegonial neck. The central cell enlarges considerably in size and its nucleus divides to form a small **venter canal nucleus** and a large **egg nucleus** . The egg of *Cycas* is the largest amongst the living plants. It is about 0.5 mm in diameter in *C. circinalis.* The mature archegonium consists of 2-4 **neck cells** and an **egg.** The venter is surrounded by a nutritive jacket of cells formed by the gametophyte cells. This jacket is called archegonial jacket.

Fertilization

The pollen tube reaches the archegonial chamber by breaking the nucellar passage. As it is filled with the fluid of high osmotic pressure, it bursts and releases its contents, including the male gametes, into the archegonial chamber. After releasing the contents, the pollen tubes become flaccid. As soon as the male gamete comes in contact with the neck cells of the archegonium, it is sucked in violently. Normally, only one male gamete enters the archegonium. The nucleus of the male gamete fuses with the egg and thus a **zygote** is formed. If per chance more than one male gametes enter in an archegonium, all except one, disorganise.

GINKGOPHYTA

Introduction & Evolutionary History

The division Ginkgophyta has one class, one order, one living genus *Ginkgo*, which has one species *G. biloba*. This single living plant is the sole representative Ginkgophyta.

Ginkgophyta is an ancient plant group about 250 million years old. The first fossils of the *Ginkgophyta* have been recorded in the Permian period. The group flourished in the Mesozoic but declined very fast in the cretaceous period.

Ginkgo biloba has existed for about 150 million years and has been rightly called the **living fossil**. Like *Cycas*, it has the cryptogamic character of fertilization by ciliated sperms.

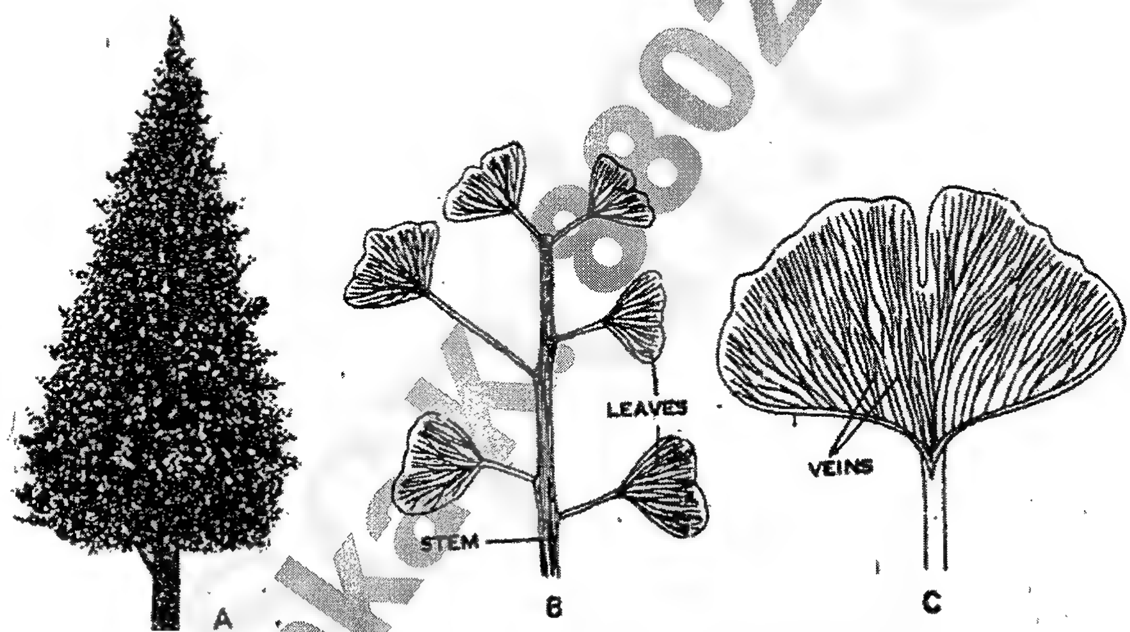

Figure 14: ***Ginkgo biloba*****. A. A mature tree; B. A branch with leaves; C. A leaf**

Distribution

The *Ginkgo* trees occur rarely in the remote forests of western China. It is considered as a sacred tree throughout Japan and China – being grown in temple gardens.

In coastal regions of the USA, the *Ginkgo* trees are grown as street shade trees.

The species is dioecious, that is the male plans and female plants are separate.

Somatic structure of the sporophyte

The adult plant resembles a conifer in general habit and may attain a height of 30 m under favourable conditions.

1. The branches are of two kinds –
   a. **Long shoots** of unlimited growth bearing scattered leaves
   b. **Dwarf shoots** or **short branches** of limited growth bearing a few leaves in cluster.
2. The leaves are deciduous, have a 5-6 cm long petiole and a broadly wedge-shaped bilobed lamina. They show free (without cross connections) dichomotous venation. The presence of free or open type of dichotomous venation resembles a similar type of venation in the leaflets of certain cycads, e.g. – *Zamia*, *Stanganeria*.
3. The stem shows an ectophloic siphonostele. The trunk and long shoots resemble *Coniferales* in showing a small pith, a thick vascular cylinder and a thin cortex, while the dwarf shoot resembles Cycadales in having a large pith, a thin vascular cylinder and a thick cortex.
4. Leaf traces are double and pass directly into the petiole.
5. Cambial activity is vigorous, producing massive secondary xylem of compact pycnoxylic type as is typical of conifers or woody angiosperms. There is also an external phellem and a considerable growth of phelloderm or secondary cortex.
6. The medullary rays are exceptionally small, one cell broad and only three cells high.
7. The cortex contains prominent mucilage canals.
8. Annual rings are not very prominent outside the vascular zone.
9. There are no resin ducts.

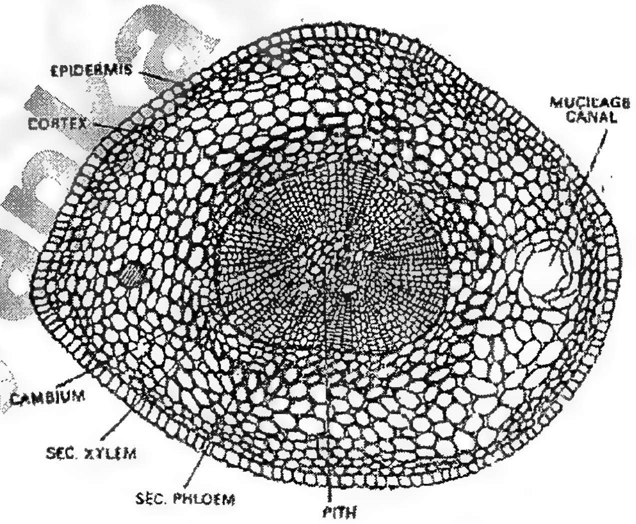

Figure 15: *Ginkgo biloba* stem in TS

Reproductive Structures and Reproduction

The plant is dioecious as the staminate and ovulate strobili occur on different plants. They occur at the ends of dwarf shoots, each in the axil of a leaf.

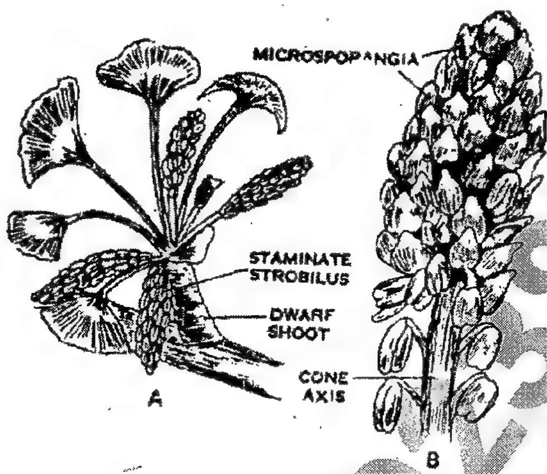

Figure 3: A. Male Strobili is *Ginkgo biloba*; B. A single male strobilus

The Male (Staminate) Strobilus

The staminate strobilus is composed of a central axis bearing many spirally arranged microsporophylls in a cluster.

Each stamen consists of a very short stalk ending in a knob (containing sac) that bears two pendant microsporangia.

The initiation of the microsporangium is that of eusporangiate type, as in Cycads.

At maturity, the microsporangium consists of a wall several cells in thickness, the remains of the tapetum and a large number of small microspores (pollen-grains).

Ovulate Strobilus

It is greatly reduced. It consists of a long stalk near whose tip, as a rule two, rarely 3-4 megasporangia (ovules) are borne.

One of these usually matures into a seed.

At the base of each ovule is a peculiar “collar” which probably represents a vestigial megasporophyll.

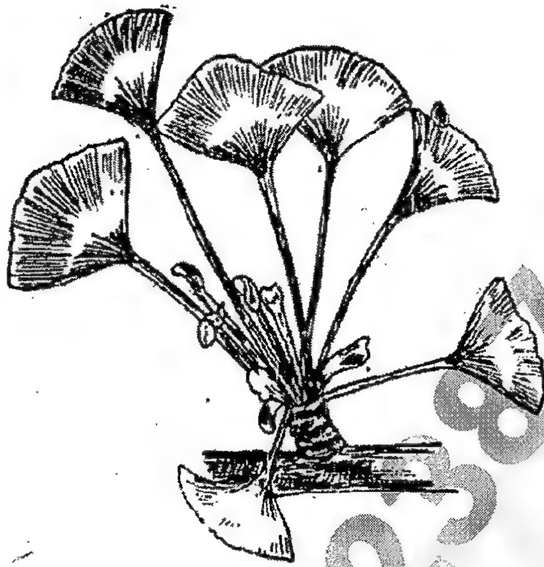

Figure 4: An ovulate strobilus in *Ginkgo biloba*

The ovule is similar in structure to that of Cycads. There is only one integument, but as the ovule matures into seed, this becomes differentiated into a fleshy outer layer, a middle stony layer, and an inner layer.

Meiosis of megaspore mother cell results in a linear tetrad of megaspores, the lowermost of which is functional.

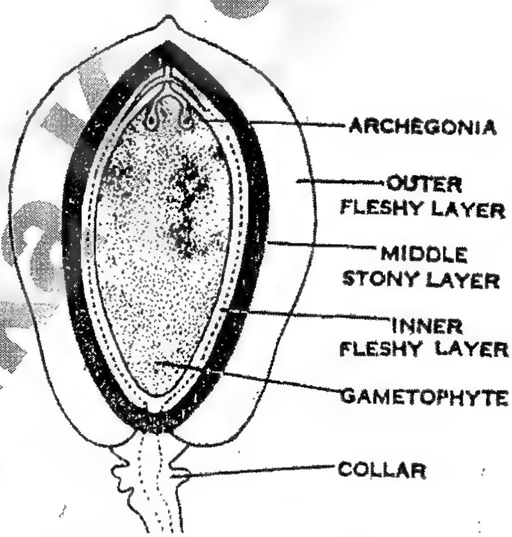

Figure 5: LS of ovule in *G. biloba*

Gametophytes and fertilization

Both the male and female gametophytes resemble closely the corresponding structures in the *Cycads* in their development and morphology.

The functional megaspore enlarges, divides and gives rise to the female gametophyte. Two or three archegonia appear in the female gametophyte, each consisting of a spherical egg-cell, a venter-canal cell and a neck of four cells. The venter canal cell ultimately disorganizes and the mature archegonium consists of four neck cells and a large egg.

The pollen-grain is the initial cell of the male gametophyte. It germinates as in *Pinus*. There are two prothallial cells, a tube cell, a stalk cell and a body cell. The body cell produces two motile sperms. The mature sperm is oval and possesses a flagellated spiral band at one end.

The distal end of the pollen-tube, as in Cycadales becomes a haustorium.

Fertilization and development of embryo may occur either on the tree or after the ovule has fallen to the ground. The embryo develops from the oospore in the usual manner. The oospore undergoes free nuclear division forming 256 nuclei, followed by wall-formation.

The mature seed of *Gingko* is brownish-yellow and about 2.5 cm, in diameter. Young seeds hang on tree resembling small fruits of angiosperms. They emit foul smell of rancid butter.

The embryo has two somewhat unequal cotyledons, of which the larger one is lobed and the smaller one is slightly notched.

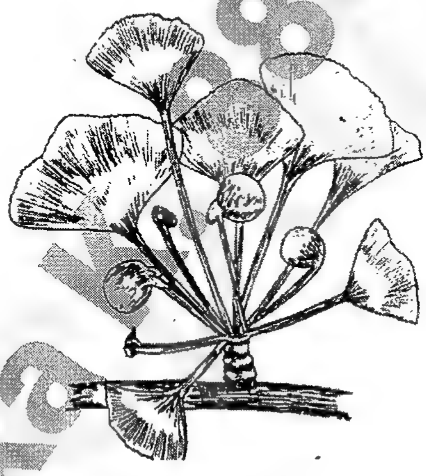

Figure 6: Seeds in *G. biloba*

Salient features of Ginkgoales

1. The order was widespread and abundant during the Mesozoic but now it is represented by the sole survivor, at present – *Ginkgo biloba.*
2. It has retained certain primitive characters of its ancestors, such as – (i) dichotomous venation, (ii) ovule with three-layered integument, (iii) pollen chamber, (iv) nucellar beak, (v) haustorial pollen-tube containing two ciliated sperms, (vi) large nutritive female gametophyte, bearing archegonia with exceptionally large eggs, and (vii) extended period of free nuclear division during early embryogeny. The mature seed in both Ginkgo and cycads consists of an endoscopic embryo with two cotyledons, embedded in the tissue of female gametophyte

which in turn is surrounded by a thick seed coat. When the seed germinates the terminal portion of the cotyledons remain as haustorial structures within the gametophytic tissue.

3. Its advanced characters are – (i) ectophloic siphonostele, (ii) small pith, (iii) thick vascular cylinder, (iv) thin cortex and (v) absence of mesarch xylem as in Coniferales.
4. Characters in common with Coirdaitales include – (i) branching habit, (ii) thick vascular cylinder, (iii) venation of leaves, (iv) structure of the stamens, (v) ovule structure, (vi) swimming sperms.
5. Distinctive features – (i) form of the leaves and (ii) structure of male and female strobili.

The similarities between Ginkgo and Cycads in the sperms, male gametophyte, ovule and ripe seed are believed to reflect a comparable degree of evolutionary progress. In other respects, it is much more like coniferophytes and there is nothing in the fossil record to suggest convergence with the cycadophytes.

Differences between the sporophytes of *Cycas* and *Ginkgo*

Cycas		***Ginkgo***	
1	Plant small, palm-like, about 2-3 m in height.	1	Plant a tree, about 30 m in height.
2	Root, a tap-root; coralloid root present.	2	Root, a tap-root; no coralloid root.
3	Leaves green, ever-green,3-6 m, compound, pinnate or bipinnate, rarely dichotomous venation.	3	Leaves simple, deciduous, long-petioled, wedge-shaped, and bilobed with dichotomous venation
4	Stem unbranched, branching rare.	4	Stem profusely branched; spur (dwarf) and long shoots.
5	Pith and cortex large, xylem (wood) manoxylic, secondary growth poor and sluggish.	5	Pith and cortex scanty; xylem dense and massive (pycnoxylic), secondary growth vigorous, dwarf shoots manoxylic like cycas.
6	Strobili of enormous size	6	Strobili of small size.
7	Microsporophylls develop on compact terminal cones, bear numerous fern-like microsporangia in sori on their abaxial surface.	7	Microsporophylls develop in loose catkins each consisting of a stalk terminating in two pendant microsporangia.
8	Megasporophylls leaf-like, pinnate, bearing 2-8 megasporangia (ovules).	8	Megasporophylls not leafy or scale-like, microsporangia 2-4, borne at the tip of a long stalk-like pendunele.
9	Ovule without a collar	9	Collar present at the base of ovule representing vestigial megasporophyll.
10	Ovule with a single integument differentiated into outer fleshy, middle stony and inner fleshy layer.	10	Ovule identical.

CONIFEROPHYTA

Coniferophyta

Coniferophyta is the largest group of gymnosperms with about 52 genera and 600 species. These plants originated in the Carboniferous period. About 30 genera of the order are confined to the Northern and 14 to the Southern hemisphere and rest of the genera cross the equator on either side. They are usually long, branched and evergreen trees. The branches are usually dimorphic and bear needle like, linear or lanceolate leaves. The wood is pyconoxylic, characterized by the presence of resin canals. The micro and megasporophylls form compact cones. The male gametes are non motile and the fertilization is siphonogamous.

Family Pinaceae

Members of this family are monoecious with spirally arranged needle-like leaves. Each needle has one or two vascular bundles, enclosed within a common bundle sheath. The pollen grains are mostly winged. The female cone has numerous spirally arranged ovuliferous scales free from the subtending bract scales or adhering only at the base. Each ovuliferous scale bears two ovule on its upper side.

The life history of *Pinus* is described here as a representative of the order Coniferales.

Pinus

Systematic Position

Division: Coniferophyta

Class: Coniferopsida

Order: Coniferales

Family: Pinaceae

Pinus, one of the most important taxon of the order Coniferales, is represented by about 105 species, distributed throughout the northern hemisphere. The species of *Pinus* form dense evergreen forests in the north temperate and subalpine region.

Five species of *Pinus* occur in the Indian sub-continent; of these, four species are confined to the north east and north west Himalayan regions. The distribution of *Pinus* in India is as follows:

1. ***P. roxburghii***: (syn. *P. longifolia*, Chir pine): This species occur in the hilly regions of Kashmir, Punjab, Himachal Pradesh and Uttarakhand at an altitude of 1450-2250 meters. The tree attains a height of 35-50 meters. There are three needles in each foliar spur.

2. ***P. wallichiana*** (syn *P. excels*, Blue pine, Kail). This species grows luxuriantly in the hills of Kashmir, Himachal Pradesh and Punjab at an altitude of 1500-3300 meters. The tree attains a height of about 50 meters. There are five needles in each foliar spur. The female strobili are cylindrical.
3. ***P. gerardiana*** (Chilgoza pine): This species is common in Kashmir and Kinnaur district of Himachal Pradesh at an altitude of 2100-3300 meters. The tree is 11-20 meters high with trifoliate spurs. The seeds are 0.5—2.5 cm in length and are edible.
4. ***P. merkusii*:** This species occur on the hillocks in East Bengal at an altitude of 150-600 meters. The plant is only 3-4 meters high. There are two needles in each foliar spur.
5. ***P. insularis*** (syn. *P. khasya*, Khasi pine) This species is widely distributed in Khasya regions of Assam and Meghalaya at an altitude of 700-1850 meters. The plant attains a height of about 30 meters and the foliar spurs are trifoliate.

Sporophyte

Figure 1: *Pinus* morphology

External Morphology

The sporophytic plant body of *Pinus* is an evergreen tree. It grows luxuriantly in temperate xerophytic habitats. When young, the plant gives a typical pyramidal appearance. The pant body has a typical pyramidal appearance. The plant body is differentiated into root, stem and leaves.

Root: The primary root is a typical tap root. It does not penetrate deep into the soil. The lateral roots grow extensively and help the plant to keep firmly in the soil. Root hairs are poorly developed. The roots are covered with fungal hyphae, called mycorrhiza. The fungi present in the ectotrophicmycorrhiza are mainly the species of *Amantia, Boletus, Clavaria and Scelorodermaof* the class Basidiomycetes. They remain in symbiotic association with the roots. It has been reported that in the absence of mycorrhizal association, the death rate of *Pinus* seedlings is considerably increased.

Stem: The stem of *Pinus* of cylindrical, erect, woody and branched. The branches are monopodial and develop spirally in the axil of scaly leaves present on the stem. Such a branching gives a conical appearance to the plant.

In *Pinus* the branches are dimorphic. The two types of branches are long shoots or branches of unlimited growth and dwarf shoots or branches of limited growth.

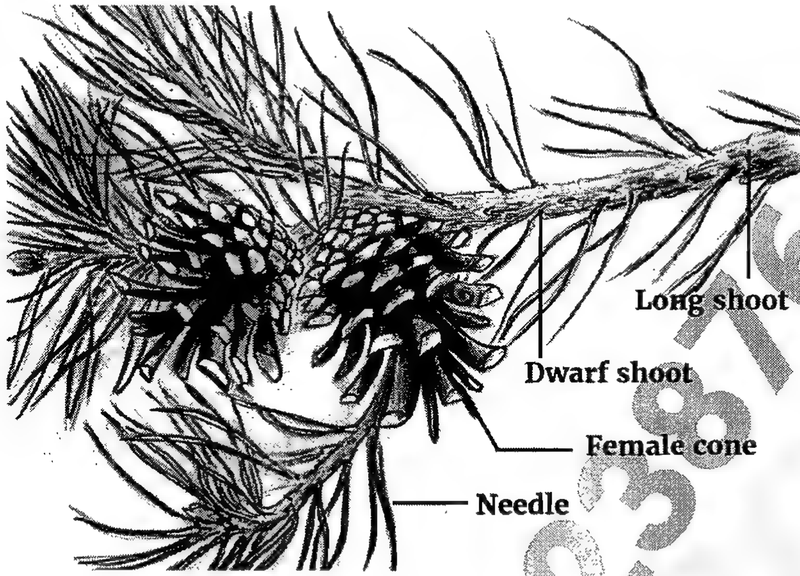

Figure 2: *Pinus* shoot system

(a) **Long shoots or branches of unlimited growth:** These branches are present on the main trunk. The apical buds of these branches grow indefinitely hence these branches are of unlimited growth. They develop in the axils of scaly leaves and spread horizontally. They shorten gradually towards the tip, thus providing a graceful pyramidal appearance to the tree. These branches *bear only scaly leaves*.

(b) **Dwarf shoots or branches of limited growth:** These branches do not have apical buds and hence show only limited growth. They are also known as **brachyblast**. They develop in the axil of scaly leaves and *bear both scaly and foliage leaves*. Dwarf shoots are shed every two or three years, leaving scars on the stem.

3. **Leaves:** The leaves are dimorphic i.e., there are two types of leaves- scale leaves and foliage leaves.

(a) **Scale leaves:** the scale leaves are dark brown, membranous, thin and small, and are present on both long and dwarf shoots. They donot help in photosynthesis. Their main function is protection of the young buds. They fall off as the branches mature. The scale leaves on the dwarf shoots have a distinct midrib and they are called cataphylls.

(b) **Foliage leaves or needle:** The foliage leaves are green, acicular and needle like. They are borne only on the dwarf shoot. A dwarf shoot with group of needle like foliage leaves is known as foliar spur. The number needles in a spur varies in different species; for instance, *P. monophylla* is monofoliar with a single needle, *P. sylvestris* and *P. merkussi* are bifoliar with two needles, *P.longifolia* and *P.gerardiana* are trifoliar with tree needles, *P.quadrifolia* is quadrifoliar with four needles and *P. wallichiana* and *P. armandi* are pentafoliar with five needles per spur. The foliage leaves are photosynthetic and remain persistent for several years. The needle like nature of the foliage leaves indicates xerophytic adaptation of these plants.

Internal Structure

Stem Primary Structure

The structure of *Pinus* stem is similar to that of a dicotyledonous stem. In trans-section the stem appears wavy or irregular in outline due to the presence of close appressing scale leaves dwarf shoots. It shows the following regions.

(i) *Epidermis*: It is the outermost layer composed of compactly arranged and heavily cutinized cells.

(ii) *Cortex*: The outer sclerenchymatous zone of the cortex forms hypodermis. It is followed by several layers of parenchymatous cells. Some cells of this zone are filled with tannins. Several resin canals are also distributed irregularly in the cortex.

(iii) *Endodermis and pericyle*: The innermost layer of the cortex represents endodermis, however, it is indistinguishable from the cortical cells. Next to the endodermis is a 2-3 layered indistinct pericycle.

(iv) *Vascular tissue*: The vascular cylinder is composed of 5-9 primary vascular bundles, arranged in a ring. The vascular bundles are conjoint, bundles are closely placed, the medullary rays (parenchymatous zone joining pith and cortex) are narrow. The tracheids are arranged in uniform radial rows. The protoxylem trachieds possess spiral thickenings, whereas those in metaxylem have reticulate thickenings. The phloem consists of sieve cells and phloem parenchyma. Some albuminous cells are also present in the phloem which are associated with sieve tubes like companion cells. One or two layers of cambium are present between the xylem and phloem.

(v) *Pith*: A parencymatous pith is present in the centre of the stem. Some pith cells are filled with resinous substances.

Secondary growth in stem

The stem of *Pinus* grows in thickenss by secondary growth. Interfascicular strips of cambium develop in the primary medullary rays in between the vascular bundles. The strips of intefascicular cambium join with the intrasfascicular cambium present in the primary vascular bundles and form a complete ring of cambium. Thus cambial ring cuts off secondary xylem towards the inner side and secondary phloem towards the outer side. The secondary vascular tissues are thus added continuously by the activity of vascular cambium and the stem increaes in girth. The primary phloem is crushed due to the pressure of secondary vascular tissues.

The cambial ring continues to form increments of secondary xylem and secondary phloem every year. The xylem ring formed in a year is differentiated into spring wood and autumn wood. The former is composed of broad tracheids and the latter of narrow tracheids. This differentiation is due to seasonal activity of the cambium. In autumn, when there is leaf fall, active translocation of water and nutrients is not required and hence the tracheids formed in this season are narrow. In spring, new leaves and branches are formed and thus there is active translocation of water and nutrients. Hence the tracheids formed in this season are broad.

The increment of a year consist of a ring of spring wood and a ring of autumn woods; the two together constitute an annual ring. The age of a plant can be calculated with the help of these annual rings.

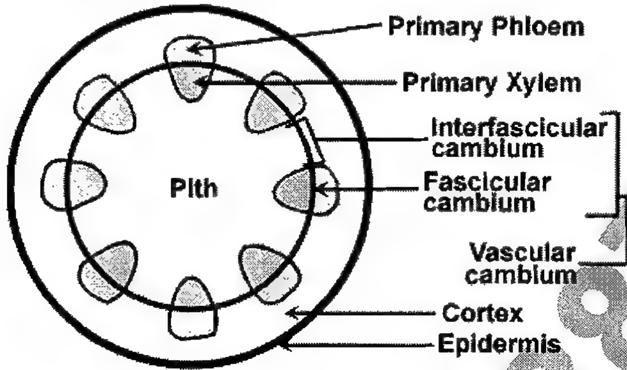

Figure 3: The meristematic cells in the intra-fascicular cambium and inter-fascicular cambium fuse and result in the formation of a continuous strip of meristem called CAMBIAL RING

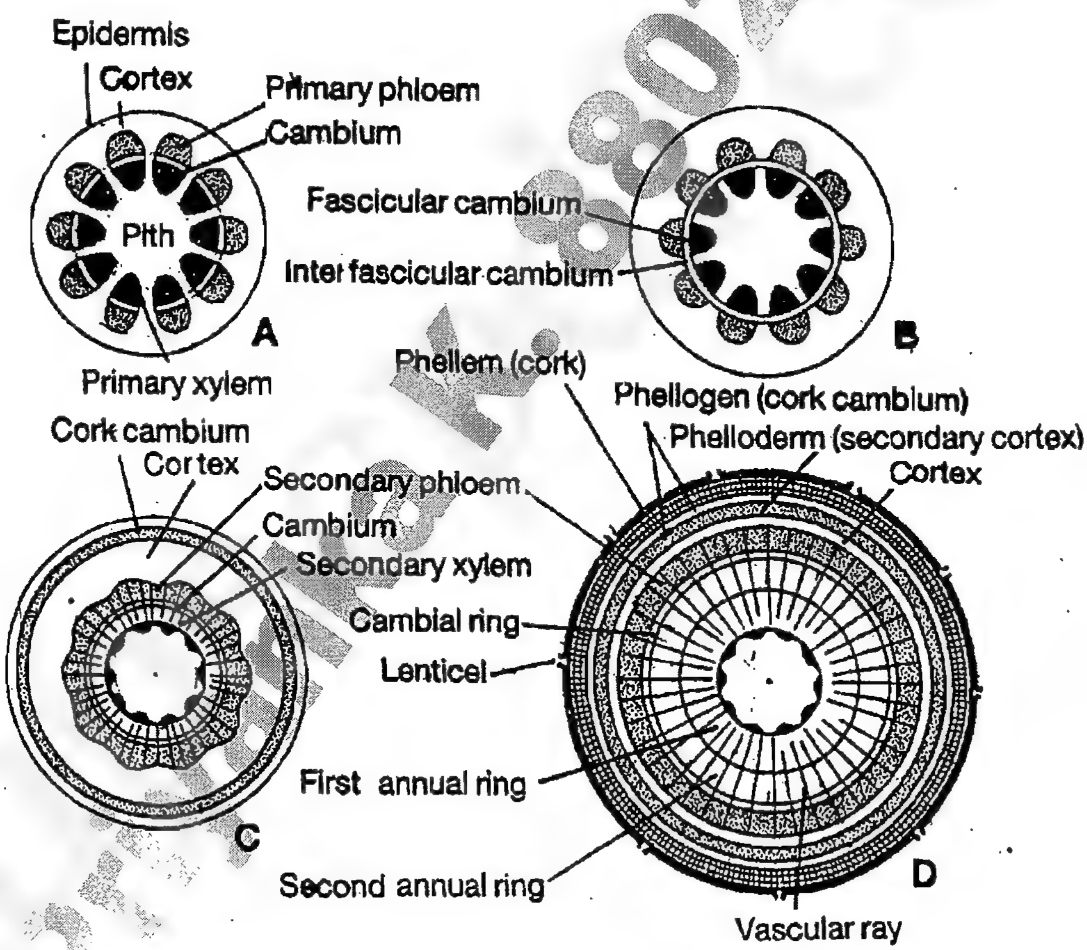

Figure 4: Schematic representation of various stages of secondary growth in *Pinus* stem

Secondary xylem: The secondary xylem which constitutes the wood of *Pinus* is pycnoxylic. The tracheids formed in the autumn are narrow and thick walled with smaller bordered pits. Thepits are present only on the radial walls. An important characteristic feature of the wood of *Pinus* is the presence of **bars of Sanio**. The occur in the form of crescentic bars in between the pits. These bars are formed by the deposition of cellulose and pectin on tracheid walls. As the wood matures, the bars are separated from the pits, and the bars of the adjacent pits are fused to form **rims of Sanio**.

The secondary vascular tissues are traversed by parenchymatous secondary medullary rays which extend from the pith to the cortex. They are formed by the cambial cells simultaneously with the secondary vascular tissues. The medullary rays are uniseriate and 2-12 cells in height.

Periderm or cork: Concurrently with the secondary growth in the vascular region, a lateral meristem, known as cork cambium, develops in the outer region of the cortex. The phellogen divides pericinally to cut cork cells (Phellem) towards the outer side and secondary cortex towards the inner side. As the stem increases in girth, the epidermis ruptures and the cork cells, form a protective covering. The cork cells are impervious to water and they check transpiration from the stem surface.

Foliage leaf anatomy

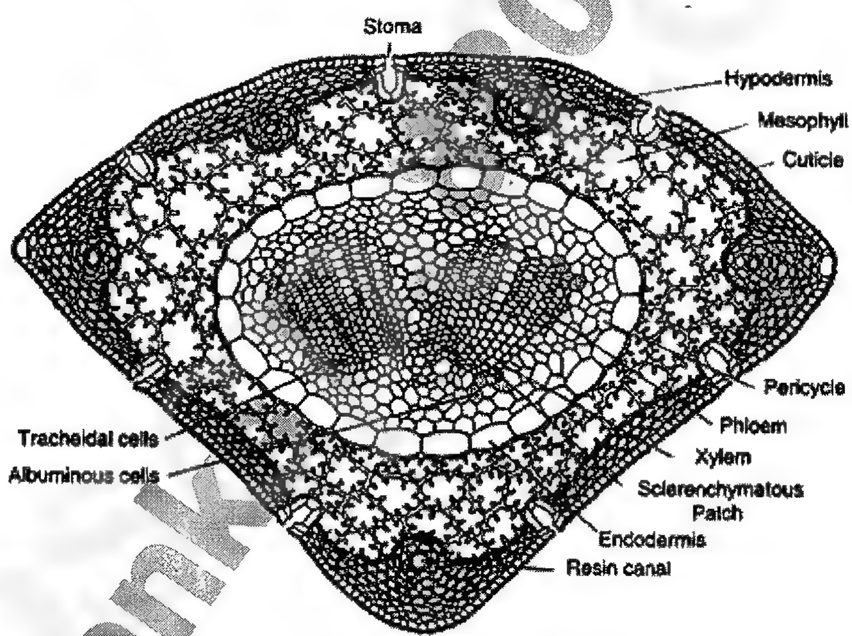

Figure 5: TS through *Pinus* needle

In transaction the outline of the foliage leaf varies in different species depending on the number of leaves in a spur. For example, it is circular in *P, monophylla* semicircular in *P. sylvestris* (with two needles in a spur) and triangular in *P.* ***lonfigolia*** and ***P. gerardiana*** (with three needles in a spur).

Epidermis: The single layered epidermis consists of heavily cutinized thick walled cells. It has many deeply sunken haplochelic stomata.

Hypodermis: The epidermis is followed by 2-3 layers of thick walled sclerenchymatous hypodermis. The hypodermis is interrupted by the presence of sub stomatal cavities.

Mesophyll: Next to hypodermis there are 3-5 layers of mesophyll tissue, composed of polygonal parenchymatous cells with dense chloroplasts and starch grains. The walls of the mesophyll cells give rise to many peg like infoldings which increase diffusive area of these cells. The structural peculiarity of mesophyll cells compensates the reduced area of the needle leaves.

There are usually two resin canals in the mesophyll, just below the hypodermis. Each resin canal has a layer of secretory epithelial cells which is surrounding on outside by sclerenchymatous sheath.

Endodermis: Inner to mesophyll, there is a layer of barrel shaped cells with prominent casparian thickening on their radial walls. This layer represents endodermis.

Pericycle: A multilayered pericycle is present next to endodermis. It consists of the following three types of cells.

(i) **Parenchymatous cells**: Most of the pericycle is composed of parencymatous cells which are densely filled with starch grains.

(ii) **Albuminous cells**: These cells occur in close contact with the phloem cells. They are also parenchymatous cells which are packed with proteins and starch grains. They do not possess pits and probably help in translocation of nutrients from mesophyll to phloem cells.

(iii) **Tracheidal cells**: These are tracheid like cells which occur close to xylem cells. These cells possess pits and help in conduction of water and minerals to mesophyll. They form transfusion tissue.

Besides the above three types of cells, some sclerenchymatous cells also occur in the pericycle which form a T-shaped girdle above the two vascular bundles in *P. roxburgii*.

Vascular bundles: The number of vascular bundles varies in different species of *Pinus*. There is only a single vascular bundle in *P. monophylla* and two in *P. roxburghii*. The vascular bundles are conjoint, collateral and open with abaxial phloem and adaxial xylem.

Narrow acicular form, thickly, cuticularised epidermis sunken stomata, sclerenchymatous hypodermis, peg like infolding in the mesophyll cells and the presence of sclerenchymatous tissue over the vascular bundles are some of the features of the leaves which indicate xerophytic nature of *Pinus*.

Reproduction

The sporophytic plant body forms two types of spores microspores and megaspores which develop into male and female gametophytes respectively. The plants are monoecious and male and female strobili are formed on the same plant. Both male and female strobili develop on the branches of the current year.

Male cone

Male cones develop in the axils of scale leaves on the branches of unlimited growth. As dwarf shoots are normally formed in the axils of scale leaves the male cones are considered as modified dwarf shoots. The male cones develop in groups just behind the apical bud. The number of cones in a cluster

varies from 15 (*P. wallichiana*) to 140 (*P. roxburghii*). The male cone is a small oval structure, about 2-4 cm long and 5-6 mm in diameter. The development of male cones starts before the female cones.

The microsporophyll is a membranous stalked and roughly triangular structure. The terminal expanded sterile part of the microsporophyll is known as apophysis. It bears two microsporangia at the base of its abaxial side. Each microsporangium has numerous microspores.

Figure 6: *Pinus* male cones in a cluster

Female cone

Female cones are formed in groups of 1-4 in the axils of the scale leaves towards the tips of long shoots of the currents year. They replace the branches of indeterminate growth. The female cone takes about three years to mature and the cones of the successive years may be seen below each year's growth of the long shoot on the terminal branches.

The first year cones are compact (1-2 cm in length) and red green with closely arranged sporophylls.

The second year cones are large and woody with sporophylls still compactly arranged.

The third year cones become loose and the sporophylls separate from one another due to the elongation of the cone axis.

The female cones are much larger than the male cones. They are usually 15-20 cm long, but in *P.coulter* they are 25-35 cm long and in *P. lambertiana* they attain a length of about 60 cm.

The female cone is much complicated in structure. It has a central axis around which many megasporophylls are arranged spirally. Some basal megasporophylls are small and sterile and the rest are fertile. The megasporophyll is a compound structure, consisting of two types of scales. (i) bract scales or cone scales, and (ii) ovuliferouos scales or seminiferous scales.

Bract scale: It is a small membranous structure which is directly attached to the cone axis just below the ovuliferous scale. At the maturity of the cone, the bract scales curve inwards so that seeds are dispersed easily. Each bract scale has a single vascular bundle with its xylem pointing upwards. The bract scale is sometimes also known as carpellary scale or cover scale.

Ovuliferous scale: It is thick, large, woody and brownish structure, attached to the dorsal surface of the bract scale. It is roughly triangular in shape and its upper broad and thick part is known as apophysis. In surface view, the apophysis is known as umbo. Two ovules are present at the base of ovuliferous scale on its dorsal surface. The micropyle of each ovule is directed towards the cone axis.

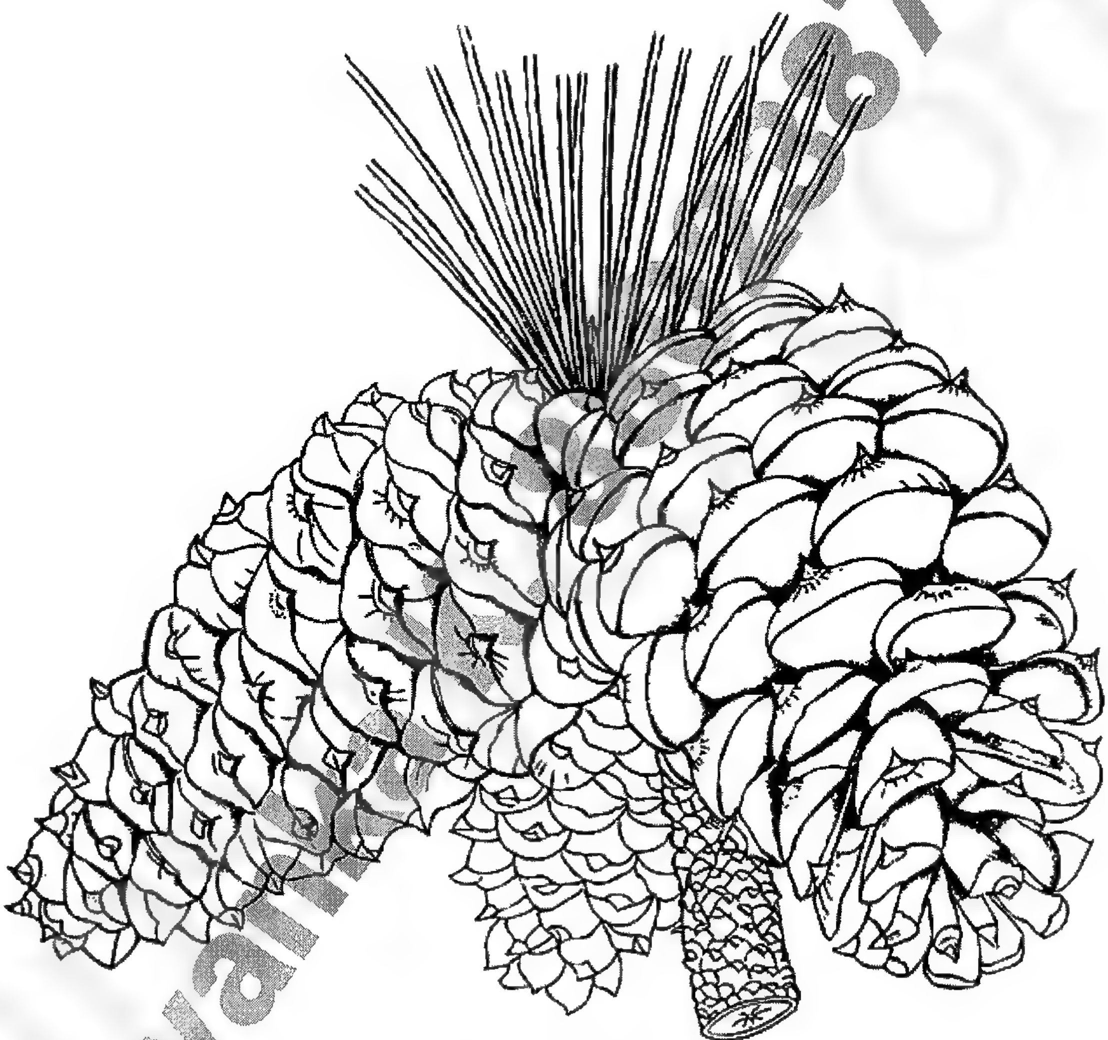

Figure 7: *Pinus* female cones

Structure of ovule: The ovule of *Pinus* is orthotropous as in other gymnosperms. The following parts can be seen in a longitudinal section of the ovule.

- **Nucellus:** It is the massive parencymatous region to the ovule.
- **Integument:** It is the thick protective covering around the nucellus. It has a very narrow aperture at the apex of the nucellus. The integuments is differented into three layers; the outer

and inner layers are fleshy and the middle layer is stony. In the upper part of the ovule a space is formed in between the integument and nucellus. This space is known as pollen chamber. After pollination, the pollen grains are collected in the pollen chamber and further development of the male gametophyte takes place inside the pollen chamber.

- **Micropyle:** It is a narrow aperture at the apex of the ovule, formed by the integument.
- **Vascular System:** The vascular system of the ovule is not very well developed. It is represented by some tracheidal elements, at the base of the ovule.

Gametophyte

Pinus is heterosporous. The microspores and megaspores are formed in the male and female cones respectively on different branches of the same plant. Both micro and megaspores are haploid and represent the first cell of the gametophytic phase. The micropores and megaspore develop into male and female gametophytes respectively.

Development of male gametophyte: The microspore is a uninucleate structure with an outer cuticularised exine and an inner thin intine. The exine expands on the lateral sides to form two balloon like structures, known as **wings**. The outer wall of the wing has reticulate sculpturing.

The germination of microspores starts in situ, i.e., they germinate while still inside the microsporangium. The microspores are released from the microsporangium after partial development of the male gametophyte. The microspores are released from the microsporangium at 4-celled stage, first and second prothallial cells, a generative cell and a tube cell. They are disseminated by wind. Further development takes place in the pollen chamber of the ovule after pollination.

After pollination the 4-celled male gametophyte reaches the pollen chamber and there it remains inactive for about 11 months. Further development of the male gametophyte starts in the next spring. The exine bursts and the intine comes out in the form of a pollen tube. The pollen tube gradually progresses towards the archegonium, penetrating the nucellar tissue. It is rich in starch grains and it may be branched or unbranched. It acts only as a sperm carrier.

The generative cell of the 4-celled gametophyte divides to form a body cell and a stalk cell. The stalk cell is larger and the body cell remains attached at its free end. The nucleus of the body cell divides to form two sperms, which are microscopic, non flagellate and ephemeral structures.

Development of female gametophyte

The megaspore is the mother cell of the female gametophyte. It remains embedded deep inside the parenchymatous tissues of the nucellus. During the development of female gametophyte, the functional megaspore enlarges in size and its haploid nucleus divides repeatedly to form 2,000-2,500 daughter nuclei. A vacuole develops in the centre of the megaspore and the multinucleate cytoplasm forms a thin layer near the periphery. Thereafter, wall formation starts from the periphery towards the centre. Thus, numerous elongated multinucleate tube like cells are formed, which are known as alveoli. Later, each alveolus divides to from many uninucleate cells. They represent endosperm or female prothallus. As in other gymnosperms, the development of endosperm in *Pinus* occurs before fertilization and hence it is a haploid structure.

All superficial cells at the micropylar end of the female gametophyte have the capacity to develop into archegonia, but only a few cells differentiate into archegonial initials. The number of archegonial initials varies in different species;

Fertilization

Fertilization takes place after a year after pollination. The pollen tube, containing four nuclei (tube nucleus stalk nucleus and two male nuclei), elongates and reaches near the tip of the archegonium, it penetrates neck cells, and when it come in the contact with the egg it release all its contents in the vicinity of the egg. Out of the two male nuclei only one fuses with the egg and the other male nucleus and the tube and stalk nuclei degenerate. The diploid zygote thus formed represents the first cell the of the sporophytic phase.

More than one archegonia in an ovule may be fertilized but the nutrients present in the ovule are sufficient only for the development of one zygote. The other zygotes, if formed, degenerate.

Economic Importance of *Pinus*

The species of *Pinus* are of considerable economic importance as the source of food, timber, oil, resins, etc.

1. The wood of *P. roxburghii* (Chir) and *P. wallichiana* (Kail) is an important timber. It is suitable for making railway sleeper, packing cases, furniture, etc. besides, it is also used for making match sticks.
2. *Pinusroxburghii, P, wallcihiana, P. insularis and P.kerkusii*are the chief source of turpentine in India. Rosins, obtained as a residue after the distillation of pine resin, are used in paper sizing, varnish making, enamels and in the preparation of plasters and ointments.
3. The roasted seeds of *P. gerardiana* (Chilgoza pine). *P.edulis*and P. *monophylla* are edible.
4. Several species of *Pinus* are grown as ornamentals in parks, gardens and in landscaping.
5. Young plants of *P. markusii* are used in the manufacture of craft paper.
6. The oleo resin obtained from *P. roxburghii* is diuretic.
7. The fossilized resin obtained from a fossil species of *Pinus* (e.g., *P.succinifera)* is known as amber. It is widely used in ornaments and decoration work.
8. The wood and female cones of *Pinus* are used as fuel.

GNETALES

Order Gnetales

The order Gnetales (sometimes treated as the plant division **Gnetophyta**) comprise three related families of woody plants grouped in the gymnosperms. The Gnetales differ from other gymnosperms in having vessel elements as in the flowering plants (**Angiosperms** or **Magnoliophytes**), and on the basis of morphological data it has been suggested that Gnetales may be the group of gymnosperms most closely related to the flowering plants. However, some recent molecular data have suggested a closer relationship of Gnetales to other gyomnosperms than to angiosperms (Bowe *et al.* 2000, Chaw *et al.* 2000, Soltis *et al.* 2002, Murphy 2007), and the conflict between morphological and molecular data has not yet been resolved.

Gnetales is one of the orders in class **Gnetopsida**. The class includes three extant genera, each under a separate order containing a single family and genus:

1. Gnetales: Gnetaceae; *Gnetum*
2. Welwitschiales: Welwitschiaceae; *Welwitschia*
3. Ephedrales: Ephedraceae; *Ephedra*

The Gnetales consist of a single genus, *Gnetum*, which are mostly woody climbers in tropical forests. However, the most well-known member of this group, *Gnetum gnemon*, is a tree. ***Gnetum*** is a genus of about 30-35 species. They are tropical evergreen trees, shrubs and lianas.

The Welwitschiales comprise only one species, *Welwitschia mirabilis*. It grows only in the deserts of Namibia and Angola. The plant is strange in having only two large strap-like leaves for all its life. These grow continuously from the base, and are usually tattered at the ends by flapping in the winds.

The Ephedrales consist of a single genus *Ephedra*, and are known as the jointfirs because they have long slender branches which bear tiny scale-like leaves at their nodes. *Ephedra* has been traditionally used as a stimulant, but is a controlled substance today in many countries because of the risk of harmful overdosing.

The order Gnetales is regarded as the most highly evolved group of gymnosperms. The order includes only one family Gnetaceae with a single genus *Gnetum*. The order is characterized by:

1. Opposite decussate leaves with unicostate reticulate venation
2. Tunica-corpus configuration of the shoot apex
3. Presence of vessels in the xylem
4. Absence of resin canals
5. Compound male and female strobili resembling inflorescences
6. Presence of perianth around the sporangia
7. A long micropylar tube

8. Tetrasporic development of female gametophyte
9. Complete elimination of archegonia
10. Absence of free nuclear divisions in embryo development
11. Dicotyledonous embryo.

Reproduction in *Gnetum*

Gnetum is dioecious, but bisexual strobili also occur rarely as in *G. africanum*.

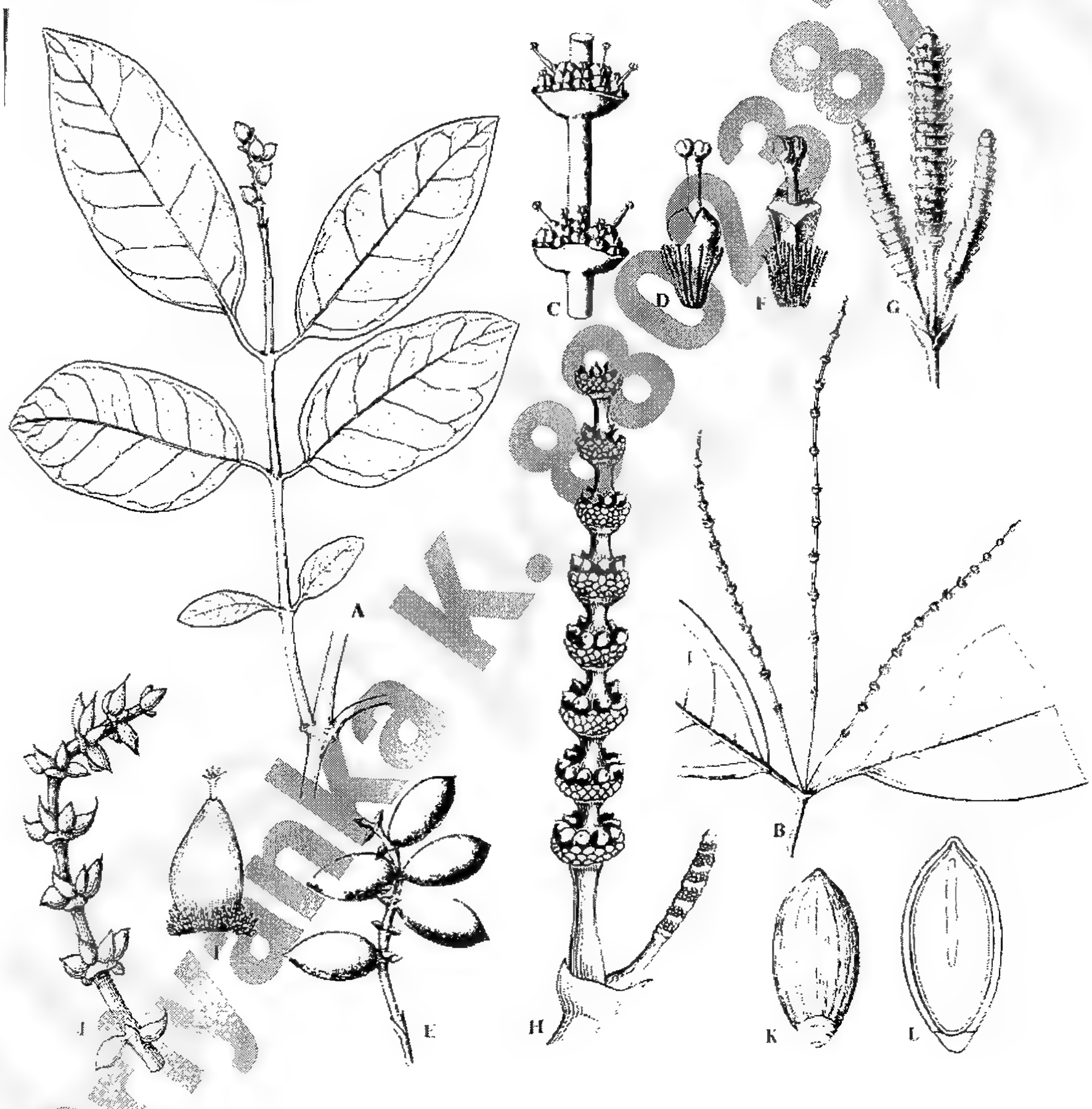

Figure 1: GNETUM. (A) A twig with leaves. (B) A twig with strobili. (C, D, F, G) A male strobilus part with microsporangia. (J) A young female strobilus (I) An ovule (E) A seed (H) A mature female strobilus (K) A seed (K) A seed in LS

The reproductive organs of *Gnetum*, often referred to as flowers, are organized into inflorescence. Both male and female inflorescences are usually axillary in position but terminal inflorescences may

also be found. A Compound strobilus consists of a stout long axis, bearing several flowers. The flowers arise in the axils of decussate pairs of bracts. There are 10-25 collars in each strobilus. They lie very close to each other because of the suppression of internodes. As leaves fall off before the strobili develop, the branches bearing strobili are leafless.

Male Strobilus

The male strobilus has a short stout axis arising in the axil of connate bracts. On the axis 10-25 whorls of bracts are present at short intervals. The whorls of bracts are present at short intervals. The bracts at each node fuse to form a cupule like structure, known as collar. In each collar there are several male flower arranges in 3-6 whorls. Above the male flowers a whorl of abortive female flowers or ovules is present. The strobilus is very compact when young, but at maturity it becomes loose as collar separate from each other due to the elongation of internodes.

1. Male flower. A male flower consists of two coherent bracts (representing the perianth) which enclose two unilocular anthers on short stalks. When the flower matures, the stalks elongate and the anthers are pushed out of the perianth sheath. Sometimes, two or more flowers are fused with each other.

2. Development of microsporangium. The development of microsporangium is of eusporangiate type. There are two or more hypodermal archesporial cells in the young microsporangium. They divide periclinally into outer primary wall cells and inner primary sporogenous cells. The tapetum is derived from the sporogenous tissue and not form the wall layers. The tapetal cells are usually binucleate, but they unite to form polyploid nuclei with many nucleoli. The primary wall cells divide repeatedly to form the epidermis and a middle layer. There is no endothecium.

3. The sporogenous cells divide in the all possible planes and form numerous spore mother cells. Each spore mother cell undergoes meiosis and forms four haploid microspores, arranged in a tetrahedral tetrad. At this stage, tapetal cells degenerate. As the microsporangium matures, all cells between the epidermis and spores break down. The anthers dehisce by longitudinal slits to release pollens.

Female Strobilus

Like male strobilus, the female strobilus also has a stout axis with several collars arranged one above the other at short intervals. A whorl of 4-10 ovules is present above each collar. All the ovules develop at the same rate initially but subsequently the growth of most of the ovules is arrested and only a few are able to mature into seeds.

1. Female flower. The female flower consists of a short stalk and an ovule (megasporangium). The ovule has a prominent nucellus protected by a three-layered envelope. The innermost envelope elongates very much and forms a long micropylar tube. A rudimaentary pollen chamber is present at the tip of the nucellus. Nucellar beak is absent.

2. Morphological nature of the envelope. The morphological nature of the envelope of the ovule is long debated and several views have been put forward from time to time. Some of these views are as follows.

A. Van Tieghem (1869) suggested that the outer envelope is equivalent to an ovary or a structure analogous to ovary and the inner two envelopes represent the two integuments of the ovules.

B. Strasburger (1872) considered that the three envelopes are formed by the splitting of a single integument.

C. Beccari (1877) was of the opinion that the two inner envelopes represent the two integuments as in the angiosperm ovule and the outer most envelope represents the perianth. Coulter (1908) also supported this view

D. Lignier and Tilson (1912) and Thompson (1916) were of the opinion that the outer two envelopes represent the perianth and the inner most is equivalent to an angiospermic ovary.

E. Vasil (1956) observed that in some specimens of *G. ula* where the innermost envelope is abortive or partially developed the middle envelope develops into micropylar tube (or 'style') in its place. Sometimes the middle as well as the inner envelopes were observed to grow into microplylar tubes or 'styles'. Following Tilson (1912) and Thompson (1916), she regarded the inner and the middle envelopes as ovaries because of their capacity to form styles.

3. Vascular supply. The main axis of the female strobilus has 12-24 bundles. Each of these bundles gives off a pair of branches which supply the outermost envelope.

4. Development of megasporangium. In the hypodermal region of the nucellus, an archesporium of two or four cells is differentiated almost at the time of the development of the innermost envelope. The archesporium divides to form primary parietal cells and sporogenous cells. The primary parietal cells along with the cells of nucellar epidermis divide repeatedly and form a massive nucellar tissue above the sporegenous cells. The sporogenous cells either directly function as spore mother cells or may undergo few mitotic divisions. The spore mother cells are arranged in long rows. The megaspore mother cells undergo two successive meiotic divisions to form four nuclei which are not separated by walls. Since no walls are laid down, all the four megaspore nuclei remain within the mother cell and take part in the development of female gametophyte. The female gametophyte is thus tetrasporic as in some angiosperms.

Some earlier workers reported that normal tetrads of megaspores are formed in *Gnetum*. But the recent studies have conclusively shown that tetrad is never formed and the degenerating mother cells were perhaps taken into consideration as non-functional megaspores.

Gametophyte

Microspores and tetranucleate megaspores develop into male and female gametophytes respectively.

Development of male gametophyte

The microspore (pollen grain) represents the earliest stage of the male gametophyte. It is roughly spherical, uninucleate and is enveloped by a thick and spiny exine and a thin intine. Mirospores are shed at 3- nucleate stage.

In the development of male gametophyte, the microspore nucleus first divides into two daughter nuclei; one of these nuclei divides again so that three nuclei are formed, which lie free in the cytoplasm. These nuclei are called prothallial nucleus, generative nucleus and tube nucleus. At this stage pollen grains are released and further development takes place in the pollen chamber.

However, *some workers believe that there is no prothallial cell.* The first division of the microspore nucleus gives rise to a tube nucleus and a generative cell nucleus; and the latter divides further into a body cell and a stalk cell. The stalk cell remains in the grain and only the body cell and the tube nucleus enter the pollen tube. It is believed that in complete elimination of prothallial cell, *Gnetum* approaches the angiospermic condition, where usually there is no prothallial cell.

The tip of the micropylar tube exudes a drop of sweet fluid to which microspores are carried. As the drop shrinks due to evaporation, microspores are caught in it and ultimately reach the top of the nucellus.

The two sperm nuclei differ somewhat in size, and it is believed that the large one is functional and the other disorganizes. The two nuclei of equal size have also been observed, but usually one of them is functional.

Development of female gametophyte

The megaspore is the first cell of the female gametophyte. The development of female gametophyte begins with a series of free-nuclear divisions. The number of nuclei formed is 256 in *G. gnemon,* 512 in *G. africanum* and about 1500 in *G. ula*. At this stage, the female gametophyte elongates towards the chalazal end. It has a large central vacuole and the free nuclei are arranged in the peripheral layer of the cytoplasm. Wall formation takes place at the chalazal end but nuclei remain free at the micropylar end.

Archegonia are absent in *Gnetum*. Some of the free nuclei of the gametophyte at the micropylar end represent eggs. They can be distinguished from other nuclei by their larger size.

Fertilization

The microspores (pollen grains) present in the pollen chamber germinate to form pollen tubes which grow through the tissue of the nucellus. The tube nucleus migrates into the pollen tube first and it is followed by generative cell which soon divides in the pollen tube to form two male cells. As soon as the pollen tube comes in contact with the embryo sac, two or three nuclei of the female gametophyte enlarge and become three to four times larger than the normal vegetative nuclei. The pollen tube enters the female gametophyte and ruptures to liberate the male cells. Usually, one of the male cells fuses with an egg and forms zygote. Sometimes, the second male cell may also fuse with the second nucleus of the female gametophyte and in such cases two zygotes are formed.

Relationships of *Gnetum*

Gnetum resembles with other Gymnosperms on the one hand and with Angiosperms on the other.

Resemblances with gymnosperms

Gnetum shares the following characters with Gymnosperms.

1. Ovules are naked and there is no structure that can be called ovary
2. Style and stigma are absent.
3. A prothallial cell is present in the male gametophyte.
4. A small pollen chamber is present in the nucellus; microspores enter the ovule through the micropyle and get directly lodged on the nucellar surface.
5. Pollination is anemophilous.
6. The endosperm is a haploid or polyploid tissue and starts developing before fertilization.
7. Presence of simple or cleavage type of polymbryony.
8. Xylem tracheids are with borderd pits
9. Sieve cells are present in the phloem but companion cell is totally absent

Resemblances with angiosperms

Gnetum has long held a key position in any discussion relating to the origin of angiosperms. Arber and Parkin (1907) considered Gnetales as the gymnosperm most closely related to angiosperms. Both were derived from a common stock – Heminagiosperms; and had parallel evolution. Thompson (1916) also shared the view that the ancestors of angiosperms were not remote from *Gnetum*. According to Hagerup (1934), there is a strong affinity between Gnetales and Piperaceae and differences between these two groups are of minor significance.

Some important features which *Gnetum* shares with angiosperms are as follows.

1. In general habit sporophyte of *Gnetum* (climber or tree like) resembles angiosperms.
2. The leaves of *Gnetum* are broad and green with reticulate venation and opposite decussate arrangement as in angiosperms.
3. All the main types of sclereids found in angiosperm also occur in *Gnetum*.
4. The development of stomata in *Gnetum* is similar to that of angiosperms.
5. The short apex organization of *Gnetum* is similar to that of angiosperms.
6. Vessels similar to those of angiosperms occur in the secondary wood of *Gnetum*, though their mode of development is different.
7. The embryo- sac of *Gnetum* is tetrasporic as in many angiosperms.
8. There is complete elimination of archegonia in the female gametophyte of *Gnetum* as in angiosperms.
9. In the occurrence of free-nuclear divisions in the embryo sac, *Gnetum* is on the angiospermic line.
10. The embryo of *Gnetum* has two cotyledons like that of a dicotyledonous embryo.
11. The male and female reproductive organs of *Gnetum* are more close to angiosperms than Gymnosperms.

Gnetum resembles angiosperms in several respects such as habit, presence of two cotyledons, reticulate venation of leaves, presence of vessels in the secondary wood, catkin like inflorescences as in some Amentiferous angiosperms, the reduction and loss of archegonium in the female gametophyte, and the presence of two integuments in the ovule. Thus, at one time *Gnetum* was considered as closely allied to angiosperms and their possible ancestors.

However, it has been subsequently shown that many of these resemblances are superficial. Angiosperms are considered to have been derived from polycotyledonous rather than dicotyledonous ancestors. There is a general tendency towards reduction in gametophyte not only within Gnetales but among the vascular plants as a whole.

The development of vessels in G*netum* and angiosperms is quite different. In angiosperms perforation of vessels arose through the dissolution of pit membranes in scalariform bordered pitting, whereas in *Gnetum* they developed through modifications of circular bordered pits.

The resemblances between the inflorescences of *Gntum* and Amentiferous angiosperms are superficial. It is now generally believed that Amentiferae have reduced flowers which are highly evolved. The primitive angiosperm flower was a bisexual strobilus with a well developed perianth and numerous free stamens and carpels. It is difficult to derive such flowers from unisexual, scaly-bracteate, compound strobili of *Gnetum*. The resemblances between *Gnetum* and angiosperms in habit, reticulate venation and the presence of double integument in the ovule are not enough to suggest their relationships.

PLANT FOSSILS & THEIR STUDY

Introduction to Palaeobotany and fossils

Palaeobotany deals with the study of fossil plants preserved in the rocks of various geological periods.

The word *fossil*, derived from a Latin word *(fossilis*, dug out) meaning "something dug up," refers to the preserved remains or traces of ancient life.

There are two major classes of fossils:

1. Body Fossil
2. Trace Fossil

A body fossil is the mineralized or otherwise preserved physical remain of animals, plants, and other organisms buried in the earth's crust during the different ages and periods of its formation.

A trace fossil, on the other hand, does not have any body part preserved. It is also known as *Ichnofossil*. It can be defined as fossil prints or marks left by living organisms. Tracks, footprints, burrows, and other marks are examples. From many types of ichnofossils the maker organism is unknown.

How are the fossils formed?

During the period between the cooling of the earth and modern times, the earth's crust has experienced several revolutions, involving widespread changes in its topography, viz.

- redistribution of land and water
- elevation of submerged land
- submergence of elevated land *etc.*

During all these and several other types of upheavals, sedimentation of whole organisms, fragmentary materials and organic remains at bottom of lakes and oceans and even at the land surface (in the form of burial *etc.*) routinely occurred. The sediments gradually became transformed to rocks (sedimentary rocks), with the plant and animal remains in them preserved in the form of fossils.

Two major factors are involved in the preservation of plant and animal bodies in the form of fossils:

1. rapidity of burial; and
2. prevention of normal decay.

A combination of these two factors often occurs in the case of burial in stagnant water, complete burial under fine-grained sediment, or rapid infiltration of mineral substances into the cell walls. In any of these cases, the quantity of available oxygen is diminished.

The right conditions for fossilization are exceptional. In most cases an organism will not fossilize.

The best-preserved fossils form when the organism is quickly buried. If the organism is not buried quickly, external factors such as scavengers, decay and the weather can deteriorate the quality of the fossil to be. As already mentioned, the fast burial of organisms occurs mainly in sediments of watery environments (i.e. clay, sand in rivers and oceans). Fossils of land animals are rarer. On land some major catastrophe like a volcanic eruption or flashflood may bury the organism fast enough with sediment.

The best parts to be fossilized include mostly only the harder parts, such as wood, shells or skeletons. However, if the organism is buried in an anoxic environment, even the soft parts can be preserved. In case of plants, only certain parts are resistant to decay and these, when properly buried in mud and sand, get transformed to fossils in consolidated sediments. Pteridophytes and Gymnosperms have been found in large numbers in fossil state, while bryophytes, algae and fungi which have delicate parts, are seldom encountered as fossils.

After burial it depends on the chemical composition of the sediment whether the organism is well preserved or not. In the sediment chemical and mineralogical composition of the fossil can be altered. The internal structure may remain preserved or the material can be dissolved in water. In this instance the cavity can later be filled up by another mineral. In this case the internal structure is lost.

After fossilization the fossil is buried deeply in the earth. Geological processes such as volcanism and mountain building the fossil can come to the surface by erosion of the overlying layers. Then we can find the fossil at the surface.

Kinds of plant fossils

Using the broader mode of classification of fossils the palaentologists identify the following types of fossils.

(1) Permineralization or Petrification: is the occurrence of decay of organic substances and filling of mineral material into every cavity of the organism, still retaining most information about the fossil.

(2) Compressions: the two-dimensional compression which retains organic matter of the organism.

(3) Impressions: the two-dimensional imprint most commonly found in silt or clay, without organic material present.

(4) Casts & Molds: caused by deposits of sediment in cavities of organism, resulting in a three dimensional model.

(5) Compactions: preservation of organic material with slight volume reduction.

(6) Molecular fossils: deals with chemical data, preserving organic material, but providing no information concerning the structure of the organism.

(7) Freezing: ideal fossils that are rare, everything up to internal organs are preserved in cold storage.

(8) Amber: biological specimen that is encased in the hardened resin of a tree, in which the entire body may be preserved.

(9) Drying & Desiccation: fossils that have been thoroughly dried.

(10) Wax & Asphalt: almost as good as freezing, but with the usage of natural paraffin.

(11) Coprolites & Gastroliths: these categories deal with the indigestable remnants of meals.

(12) Trace fossils: typically formed when an organism moves over the surface of soft sediment and leaves an impression of its movement behind.

Plant fossils fall in the following principal categories.

(1) Petrifaction *(petra,* rock; *facere,* to make): This means fossilization by cell-to-cell replacement of certain plant parts by a good number of mineral substances, of which carbonates of calcium and magnesium, iron sulphide and silica are the most common. Petrified fossils have shown the external form, internal structure, and sometimes substance of the original plant, often in great detail. In this case, before vertical pressure came into play, the plant fragments were saturated with water, containing mineral substances in solution. The mineral substances infiltrated into the plant body, and gradually separated out from the solution. In due course the water was expelled. Finally, the tissues and cells had a complete filling of solid materials, and the whole formed a solid, incompressible, hard mass. Coal balls and silicilled wood are the best examples of petrification. Coal balls remain embedded in the coal and are of varying sizes, usually about the size of potatoes. They are often very rich in the calcified remains of plant materials. Silicified stumps of wood have often been so well preserved that it has been possible to prepare thin sections of them for microscopic examination. They often reveal minute structures in extraordinary detail.

(2) Incrustation or Cast. This is a fossil with the external form as a cast. The internal structure is not preserved. Here the plant substances have disappeared and a cavity has been left. This cavity is subsequently filled with mineral matter, which forms a *cast* of the original plant. The surrounding material, the mould, forms the *incrustation.* Casts of pith cavities of hollow stems have been found. These resulted from the entry of fine sand or mud into the hollow stems. In the course of time the filling material was converted into an internal mould of the hollow stem, e.g. the pith cast of *Calamites.*

(3) Compression. In this case, the external form of the plant was modified by the vertical pressure of the sediment in which the plant material was embedded. When a plant is subjected to compression, some of its parts-leaves, seeds, fruits, trunks, *etc.* leave impressions on the rock surface. The outline of the plant or its part is left on the rock surface due to compressions.

(4) Compactions. These are plants or plant fragments compressed by vertical pressure. Masses of plant fragments without the intervening matrix such as are found in peat and coal are large-scale compactions.

(5) Impressions. The forms impressed on a matrix, as on coal and shale, which harden afterwards, are usually termed impressions. They can be characterized as Ichnofossils. The external features of plant parts are thus preserved.

Different methods used for studying fossil plants

It is laborious process and requires sufficient time.

The steps in fossil studies are as follows.

Site preparation

When a potential site is identified, it is surveyed using technology that produces three-dimensional maps and plans of potential fossil-bearing areas. Finds are plotted on virtual maps using a digital Geographical Information System (GIS).

Excavation

The type of excavation method used depends on the type of sediment, or matrix, holding the fossils.

Technicians carefully uncover fossils from rocks by removing the surrounding rock using delicate drills, including power tools called airscribes, which use compressed air. Specimens are numbered and catalogued with reference to their position vertically and horizontally in the site. Photography and making drawings of stratigraphic sections are important activities during the excavation.

In the laboratory

After a fossil has been prepared and cleaned, it is studied in the laboratory.

There are many ways of examining fossils in detail. Significant fossils can be measured using callipers.

Binocular light microscopes are used to look at surface features. A scanning electron microscope (SEM) is used for detailed, high magnification analysis. Trace element and isotope analysis of soils and fossils provides information about the environment.

Researchers can study the internal anatomy of fossils without damaging the material by using X-ray analysis (radiography).

CT scans (using computed tomography) provide detailed internal images of fossils.

Methods for the petrified specimens: Usually the petrified specimens are cut in serial sections which give an idea of the actual structure of the fossil plant. These petrified pieces are cut into very fine slices by different methods. In one method each such piece is attached to glass plate and grounded to sufficient thinness and thereafter studied under the microscope.

Another improved method of the study of these petrified specimens is to prepare the films of the material by special techniques. The methods of preparing thin films are as follows: First of all the surface of the section of the petrified material is made smooth. If the material consists of calcium carbonate, then on the smooth surface of the slice a film of 5 percent hydrochloric acid is allowed to act for five minutes.

If the slice of the petrified material is silica then the film of 10 percent hydroflouric acid (HF) is allowed to act on the smooth surface for ten minutes so that the silica is dissolved. The surface 6f the petrified section by the action of these acids becomes rough on account of the dissolution of the mineral matter. If any organic matter remains on the surface, now put hot gelatin on the surface.

As soon as the things dry up, they are removed and studied under the microscope. This process may be successful only in the case when organic matter is left in petrified specimens. In case where organic matters are already decayed, such preparations are never good.

Dating

Scientists date fossils using various techniques.

Researchers are able to get a rough time-frame for fossils by relating them to the rock layers (stratigraphic sequences) in which they are found.

Where fossils are found in association with volcanic ash deposits,

their age can be determined using potassium-argon dating. This method is based on the fact that after volcanic rock cools some of the radioactive isotope potassium-40 (K-40) decays to the gas argon-40 (Ar-40), which is then trapped within the rock. Uranium Series Dating is also based on the decay of radioactive isotopes, in this case by measuring the proportions of uranium to lead or uranium to helium in an ancient sample.Electron Spin Resonance (ESR) dating is based on natural radioactivity.

Radiocarbon dating: Radiocarbon dating is of limited value since it cannot be applied reliably to samples that are older than about 50,000 years. This technique is based on the fact that all living organisms have a mixture of stable 12C and radioactive 14C isotopes (absorbed from the atmosphere). After death, organisms do not absorb 14C any longer, and the remaining radioactive isotopes decay at a known constant rate. By measuring the proportion of 14C relative to 12C in an ancient organic sample, it is possible to calculate its age.

Reconstruction

The fossils are mostly pieces of plants. It is very rare that entire plant could have preserved. This way, only pieces can be studied. In such type of study the individual pieces are given botanical names, just as in living plants; the botanical names of the fossil plants are not so significant as those of living ones.

As they are represented by the pieces of the plants and, therefore, their generic names would be according to stem, leaf and root or any reproductive structure. The stems are usually given the generic names which end with 'dendron' (tree) or 'xylon' such as, Lygenodendron or Cladoxylon. The leaves end with 'pteris' or 'phyllum' and reproductive parts end with strobilus. This way, the paleobotany is the study of the parts of fossil plants and in certain case marvellous results have been obtained.

In the case of Lyginopteris, one of the Cycadofllicales of Carboniferous period which was found in pieces and later on the palaeobotanists supported that all the pieces belonged to the particular plant. Later on after few years the complete intact plant was found.

Applications of fossils & palaentology

The sedimentary rocks have been divided into different geological periods on the basis of their fossil contents. Palaeontology, which deals with plant and animal fossils, gives us a glimpse of the occur-

rence and nature of ancient life-flora and fauna-in past geological ages. It tells us precisely about the period of the earth's history when particular types of plants and animals came into existence, flourished and became extinct, and also their geographical extent. The study of fossils is, thus, of utmost importance in tracing the evolutionary sequence of flora and fauna-appearing, disappearing, and giving rise to more organized forms in successive stages.

Palaeontology is directly correlated with the stratigraphy of the earth, i.e. the formation of the earth's strata in the different periods. It has, therefore, been possible to determine the age of the particular strata from the occurrence of fossils in them. The carbon-dating method is used to fix the age of the fossil.

Fossils also tell us about the extent of land, lakes and seas in the past ages. This is how it has come to be known that a vast sea called Tethys existed in the region of the present-day Himalayas possibly with some land bridges across this sea.

Palaeontology has its economic application in the exploration of minerals, especially coal, occurring in freshwater sedimentary formations (Carboniferous), and oil (petroleum) possibly derived from marine, planktonic flora and fauna (in the Eocene age). It is known that an ancient (carboniferous) flora played an important part in the formation of coal. In India, the coal beds of Raniganj and Jharia are of the Permian age. Palynology, dealing with fossil spores and pollen grains, is of great value in determining and comelating coal seams and sedimentary beds of both freshwater and marine origin.

GEOLOGICAL TIME SCALE

Introduction

Geologists have created a geologic time scale to provide a common time frame to describe events from the earth's evolutionary past. The practice of determining when past geologic events occurred is called **geochronology**.

The first geologic time scale was proposed in 1913 by the British geologist Arthur Holmes (1890 - 1965). This was soon after the discovery of radioactivity, and using it, Holmes estimated that the Earth was about 4 billion years old.

Though the geologic time scale is generally agreed upon and used by scientists around the world, every few years, the numerical time scale is refined based on new evidence, and geologists publish an update.

The currently accepted time scale

The current **geologic time scale** is a chronologic schema relating stratigraphy to time used by geologists and other scientists to describe the timing and relationships between events that have occurred during the history of Earth. All the standard stratigraphic divisions are based on fossil stratigraphies (biostratigraphy).

The geological timescale commonly subdivides the past 4700 million (4.7 billion) years (since the Earth's formation) into hierarchical divisions; eras, periods, and epochs (Harland *etal.*, 1990). The largest defined unit of time is the **supereon**, composed of **eons**. Eons are divided into **eras**, which are in turn divided into **periods**, **epochs** and **ages**.

The terms related to Geologic Time Scale are defined below.

1. **EON**: Two or more geological eras form an Eon, which is the largest division of geologic time, lasting many hundreds of millions of years.
2. **ERA**: Two or more geological periods comprise an era, which is hundreds of millions of years in duration.
3. **PERIOD**: The period is the basic unit of geological time in which a single type of rock system is formed, lasting tens of millions of years.
4. **EPOCH**: An epoch is a division of a geologic period; it is the smallest division of geologic time, lasting several million years.
5. **AGE**: An age is a unit of geological time which is distinguished by some feature (like an Ice Age). An age is shorter than epoch, usually lasting from a few million years to about a hundred million years.

The table presented below provides the major changes in the plant record across the geological period.

Age	Era	Period	Epoch	Characteristic Plant Association	Climatic Inference
5,000–10,000 yrs.	CENOZOIC	Quaternary	Holocene	Modern flora	Retreat of ice sheet
2.5 m.y.			Pleistocene	Redistribution of floras	Successive glaciations
7 m.y.		Tertiary	Pliocene	Spread of grasslands, caused local restriction or extinction of some species	Elevation of Andes, climatic changes in temperate latitude
26 m.y.			Miocene	Establishment of present-day forest association	Continental uplift, rise of Alps, Himalayas
38 m.y.			Oligocene	Widespread occurrence of relic taxa like *Metasequoia*	Mild-temperate climate
54 m.y.			Eocene	Many angiosperm extinct and appearance of new types. Distinct forests in Northern and Southern latitudes	Subtropical climate, with heavy rainfall
65 m.y.			Palaeocene	Primitive angiosperms like Magnoliaceae, Lauraceae, Junglandaceae	Trend from temperate to mild-subtropical climate, seasonal variations
141 m.y.	MESOZOIC	Cretaceous	Upper Lower	First appearance of angiosperm	Climate tending to be uniform, temperate
195 m.y.		Jurassic	Upper Middle Lower	Cycads, ginkgos, conifers, ferns, cycadeoids, some pteriodosperms	Uniform, mild climates from North to South Poles
225 m.y.		Triassic	Upper Middle Lower	Rise of cycads and ginkgos. Diversification of conifers and ferns	Arid to semi-arid savanna-type climate

Age	Era	Period	Epoch	Characteristic Plant Association	Climatic Inference
280 m.y.	PALAEOZOIC	Permian	Upper Lower	Diversification of Southern hemisphere glossopterids, Extinction of arboscent lycopods and sphenopsids	Cooler and drier climates with extensive glaciation in Southern hemisphere
325 m.y.	PALAEOZOIC	CARBONIFEROUS – Pennsyl-vanian	Upper Middle Lower	Origin of conifers, formation of great arboreal swamp forest	Uniformly warm, humid climate
345 m.y.	PALAEOZOIC	CARBONIFEROUS – Mississi-ppian	Upper Lower	Primitive ferns, seed ferns, arborescent lycopods, *Calamites*	Warm, equable climate
395 m.y.	PALAEOZOIC	Devonian	Upper Middle Lower	Diversification of vascular plants, establishment of heterospory and seed habit	Heavy rainfall and aridity, extensive inundation of continents
435 m.y.	PALAEOZOIC	Silurian	Upper Lower	First vascular land plant *Cooksonia*	Mild climate low-lying continents with epicontinental flooding
500 m.y.	PALAEOZOIC	Ordovician	Upper Lower	Abundance of red and green algae	Warm, mild climate, epicontinental seas
570 m.y.	PALAEOZOIC	Cambrian	Upper Middle Lower	Abundance of blue-green, green and red algae	Warm and equable
2,500 m.y.	PRE-CAMBRIAN	Proterozoic		First cell bacteria, growth of blue-green algae (stromatolite), and possibly green algae	Warm, organic evolution
3,800 m.y.	PRE-CAMBRIAN	Archaeozoic			
4,700 m.y.	PRE-CAMBRIAN	Hadean		No fossil record	Chemical evolution. Hot orign of earth.